Natural History and Resource Use of Four Amazonian Tadpole Assemblages

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ABSTRACT   Four tadpole assemblages were studied during the 1989–90 rainy season at the Reserva Cuzco Amazónico located on the Río Madre de Dios, in Amazonian Peru. The ponds varied in size, depth, permanency, light penetration, alkalinity, hardness, and number of anuran and non-anuran species present but were similar in water temperature, dissolved oxygen, and pH. While sets of these characteristics appeared correlated among ponds, none of the characteristics was related to tadpole species richness, evenness, or diversity.

Netting sampled 3820 tadpoles of 19 species, plus 1413 individuals of one species of crab, two species of aquatic insects, and 10 species of fish. Patterns of differential use among anuran species were found for most of the resource dimensions. Macrohabitat and time within the rainy season appeared to be the most important resource dimensions, followed by food (represented by ecomorphological guild), microhabitat (level in the water column), and diel time period. Some species demonstrated associations between microhabitat, diel time period, and development. Tadpoles of 25 other anuran species known to occur at Cuzco Amazónico were not encountered. These species probably use other macrohabitats, but not other time periods, because most aquatic habitats exist only during the rainy season. Rainfall seems to be the most influential factor in determining the patterns of resource utilization by tadpoles, because it determines the degree to which the macrohabitats can be utilized temporally.

RESUMEN   Se estudiaron cuatro agregados de renacuajos durante la estación lluviosa de 1989–90 en la Reserva Cuzco Amazónico, localizada en el Río Madre de Dios, Perú. Las charcas diferían en tamaño, profundidad, permanencia, penetración de la luz, alcalinidad, dureza y número de especies de anuros y no anuros presentes, pero eran similares en temperatura del agua, concentración de oxígeno disuelto y pH. Mientas que ciertos conjuntos de estas características mostraron correlación entre las charcas, ninguna de estas variables estaba relacionada con la riqueza, equitabilidad o diversidad en especies de renacuajos.

Se capturaron con red 3820 renacuajos de 19 especies, así como una especie de cangrejo, dos especies de insectos acuáticos y 10 especies de peces, totalizando 1413 individuos. Se encontraron diferencias en los patrones de uso para la mayoría de los recursos utilizados por los renacuajos. El macrohábitat y el tiempo dentro de la estación lluviosa parecen ser las dimensiones más importantes, seguidas por el alimento (representado por gremios ecomorfológicos), microhábitat (nivel en la columna de agua), y ritmos de actividad diaria (noche o día). Algunas especies demostraron asociaciones entre microhábitat, ritmos de actividad diaria, y estadío de desarrollo. No se encontraron renacuajos de otras 25 especies de anuros que habitan en Cuzco Amazónico. Dichas especies probablemente usan otros macrohábitats, pero no otros períodos de tiempo, pues la mayoría de los hábitats acuáticos existen sólo durante la estación lluviosa. La precipitación parece ser el factor más influyente en la determinación de los patrones de uso de los recursos por parte de los renacuajos, porque determina hasta qué grado los macrohábitats pueden ser utilizados temporalmente.

Palabras claves: Renacuajos; Agregados; Comunidades; Utilización de recursos; Historia natural; Amazonia peruana; Anuros.

Most studies of anuran communities have focused on the adult reproductive period. Many have addressed reproductive strategies and attempted to quantify adult community structure but have given tadpole assemblages little more than anecdotal attention (e.g., Inger, 1969; Crump, 1971, 1974; Creusere and Whitford, 1976; Duellman, 1978; Toft and Duellman, 1979; Aichinger, 1987; and the many studies cited in Gascon, 1991). This reflects a long outdated view that anuran communities must be organized in the adult stage because tadpoles are so similar (Inger and Greenberg, 1966). The little attention accorded tadpole assemblages is surprising, because it has been suggested that among anurans with a biphasic life cycle, selection is strongest during the larval stage (Blair, 1961; Heyer, 1973, 1979). Whereas both—i.e., groups of adults and of tadpoles—have been treated frequently as independent communities, factors acting at both levels can influence the anuran composition at a given locality. For this reason, throughout this study the term "community" will be reserved for references

to the entire set of anuran species at the study site. The term "assemblage" will be used to refer to the set of tadpole species in a given aquatic habitat in order to emphasize that the composition of a particular assemblage is not independent of factors (including stochastic ones) acting on the adult species present.

Toft (1985) reviewed studies of resource partitioning in amphibians (including larval assemblages) and reptiles, and listed six resource dimensions that encompass most known ways organisms can differ ecologically. As applied to tadpoles, these dimensions are: macrohabitat—distribution of tadpoles among aquatic habitats; microhabitat—spatial distribution of tadpoles within the aquatic habitat; food type—tadpole food type consumed; food size—tadpole food size consumed; diel time period—diel period of tadpole activity; and seasonal time—temporal distribution of tadpole occurrence, in the aquatic habitat. Any discernible nonrandom pattern in the distribution of species among resource dimensions is considered assemblage structure and is indicative of differential resource usage or resource partitioning. Many studies of naturally occurring tadpole assemblages addressed some aspect of resource partitioning; however, most examined a limited number of resource dimensions, usually seasonal time and microhabitat, and thus provide incomplete descriptions (Blair, 1961; Dixon and Heyer, 1968; Calef, 1973; Heyer, 1976, 1979; Heyer et al, 1975; Walters, 1975; Wiest, 1982; Alford and Crump, 1982; Smith, 1983; Berger, 1985; Hero, 1990; Gascon, 1991). A few studies have focused specifically on resource partitioning among tadpoles (Alford, 1986; Inger et al., 1986), but only Heyer (1973, 1974) examined all resource dimensions in a single study. Most studies found habitat partitioning by seasonal time to be the most important dimension (Dixon and Heyer, 1968; Wiest, 1982), but microhabitat (Heyer, 1974, 1976; Alford and Crump, 1982; Alford, 1986; Hero, 1990) and/or macrohabitat (Heyer, 1973; Smith, 1983; Gascon, 1991) also may be important adjuncts. Food is thought to be of minor importance in resource partitioning of tadpole assemblages (Dixon and Heyer, 1968; Calef, 1973; Heyer, 1973, 1974, 1976). Only Inger et al. (1986) found seasonal time to be unimportant; spatial occurrence and food were the most important dimensions at their uniquely aseasonal stream locality.

In summary of these studies on resource partitioning of amphibian assemblages, Toft reported that they differ from all other vertebrate assemblages because seasonal time was the most important dimension in nearly every study conducted. The sequence of mean ranks of importance of each dimension among all studies summarized by Toft are: (1) seasonal time, (2) microhabitat, (3) macrohabitat, (4) food type, (5) food size, and (6) diel time period. Because only Heyer (1973; 1974) examined all of these

resource dimensions, the sequence may be biased by the frequency with which each dimension was investigated. The results of most studies on tadpole resource partitioning subsequent to Toft's review conform to her ranking.

Resource partitioning has been addressed in studies of tadpole assemblages in both temporary (Texas—Blair, 1961; Texas—Wiest, 1982) and permanent (British Columbia—Calef, 1973; Maryland—Heyer, 1979) aquatic habitats in temperate climates. Tadpole assemblages have been studied in a wide variety of tropical aquatic habitats (e.g., Mexico—Dixon and Heyer 1968; Thailand—Heyer, 1973, 1974; Costa Rica—Heyer et al. 1975; Borneo—Inger et al., 1986; Brazil—Hero, 1990; Gascon, 1991), and comparatively between tropical and temperate habitats (e.g., Kansas/Ecuador— Berger, 1985; Maryland/Panama—Heyer, 1976). However, there have been few studies of tadpole assemblages of the most diverse frog fauna of the world—that found in the Amazonian Basin (e.g., Berger, 1985; Hero, 1990; Gascon, 1991), where resource partitioning has been shown to be more pronounced in comparison to temperate regions (Berger, 1985).

Toft attributed resource partitioning patterns to three causes—viz., competition, predation, and factors that operate independently of interspecific interactions. Both descriptive studies (Heyer, 1973, 1976; Heyer et al., 1975; Cecil and Just, 1979; Smith, 1983) and experimental investigations under artificial conditions (Brockelman, 1969; Calef, 1973; Debenedictis, 1974; Walters, 1975; Woodward, 1983; Gascon, 1992) frequently have cited predation as an important influence on natural tadpole assemblages. Most descriptive studies of naturally occurring tadpole assemblages found competition to be nonexistent or present but of minor influence (Heyer, 1973, 1974, 1976; Alford, 1986; Inger et al., 1986). However, competition has been demonstrated frequently in manipulative or artificial experimental studies and, therefore, is considered potentially important in structuring tadpole assemblages (Brockelman, 1969; Wilbur, 1972, 1976; Wilbur and Collins, 1973; Debenedictis, 1974; Smith-Gill and Gill, 1978; Steinwascher, 1978; Travis, 1980; Seale, 1980). Furthermore, experimental studies also have shown that predation and competition are interrelated (Morin, 1981, 1983, 1986, 1987; Wilbur, 1982; Smith, 1983; Scott, 1990; Sredl and Collins, 1992).

In addition to predation and competition, abiotic factors influence tadpole assemblages. Of these, seasonality, (especially with regard to rainfall) clearly explains seasonal partitioning (Dixon and Heyer, 1968; Heyer, 1973; Turnipseed and Altig, 1975; Creusere and Whitford, 1976; Toft et al., 1983; Berger, 1985; Pechman et al., 1989). Other climatic and aquatic factors can be influential as well (e.g., Alford, 1986; Inger et al., 1986; Gascon, 1991) including water pH, fluctuations of air and water tempera-

ture, and humidity (Gosner and Black, 1957; Blair, 1961; Wiest, 1982). Such physical factors become more influential in structuring tadpole assemblages with increased seasonality (i.e., latitude; Heyer, 1973). The effects of abiotic factors may be interrelated in a complex way, especially in determining the timing of adult reproduction (Savage, 1961) and, thus, temporal partitioning of the tadpole habitat. Abiotic factors also may influence interspecific associations or work in combination with them to determine tadpole assemblage structure (e.g., Heyer et al., 1975; Smith, 1983; Woodward, 1983; Scott, 1990; Sredl and Collins, 1992). Toft (1985) concluded that no single factor explains resource partitioning among tadpoles; rather the interaction among physical factors, predation, and competition produces observed patterns of resource partitioning. Moreover, the nature of the interaction among causal factors seems to vary among sites (although there have been few studies of tadpole assemblages in the Amazonian Basin for comparison) and probably from year to year.

Disparity in conclusions regarding the relative importance of the various resource dimensions and causal factors, particularly with regard to predation and competition and especially between descriptive and experimental studies, highlights the inherent complexity of tadpole assemblages and the difficulty of studying them (Scott and Campbell, 1982). More information is needed about naturally occurring tadpole assemblages, particularly in the Amazon Basin, (Heatwole, 1982; Toft, 1985; Altig and Johnston, 1989). Initial studies should be descriptive so that patterns can be recognized (Toft, 1985). This information will provide a basis for experimental investigations of the underlying causes of the patterns and their interrelationships (Heyer, 1979; Scott and Campbell, 1982).

The study reported herein focuses on tadpole assemblages in Amazonian Peru in order to address the general question of how 54 species of anurans with life cycles that include aquatic tadpoles can coexist in a tropical community. The study is primarily descriptive and the specific objectives are to (1) provide baseline ecological data and descriptive natural history of selected tadpole assemblages at a single site in Amazonian Peru throughout the duration of an entire rainy season; (2) examine simultaneously all resource dimensions (macrohabitat, microhabitat, seasonal time, diel time period, and food) previously suggested in the literature to be important in interpreting patterns of differential utilization among tadpole species; (3) examine the interrelationships among tadpole development, diel activity, and microhabitat for species with sufficient numbers; (4) examine evidence suggestive of those causal factors (competition, predation, and abiotic) potentially responsible for resource utilization patterns; and (5) compare these findings with other studies.

METHODS AND MATERIALS

DESCRIPTION OF STUDY AREA

The study was conducted from 10 December 1989 to 31 March 1990 during the rainy season at the Reserva Cuzco Amazónico, a tourist lodge and reserve on the north bank of the Río Madre de Dios, about 15 km ENE of Puerto Maldonado, Provincia de Tambopata, Departamento de Río Madre de Dios, Peru (12°33' S, 69°03' W). The western boundary of the reserve is a slow-moving stream, the Quebrada Mariposa, that empties into the Río Madre de Dios. In the adjacent forest, there was a network of about 10 km of trails that included two study zones of marked contiguous quadrats (Fig. 1). A detailed description of Cuzco Amazónico and a discussion of the biological investigations conducted there are provided by Duellman and Koechlin (1991).

The climate at Cuzco Amazónico is seasonally tropical. Records from the nearest continuously operating weather station in Puerto Maldonado during 1971–1989 indicate that the rainy season extends from October through March, with the heaviest rainfall in January and February; the least amount of rain falls in June and July. The mean annual rainfall is 2416 mm with annual extremes of 1844–3718 mm. Temperature records from 1978–1989 reveal that October is the hottest month, with a mean monthly maximum of 32.2°C. A distinct cool season corresponds to the driest months of the year (May–July). Ambient humidity peaks at night, reaching 92–99% in both seasons, and is lowest near midday.

The region is mapped as humid tropical forest, but is situated near the transition between humid tropical forest and dry tropical forest (Tosi, 1960). The mostly evergreen forest comprises terra firma and seasonally inundated forests, which differ floristically. There are fewer ferns and less herbaceous ground cover in inundated forest than in terra firma forest, but more *Heliconia* and *Calathea*. Except in areas of dense growths of these plants, the understory is more open in inundated forest than in terra firma forest (Duellman and Koechlin, 1991).

Studies by Duellman and his colleagues have produced a thorough inventory of the fauna at Cuzco Amazónico. The herpetofauna includes 81 species of reptiles and 64 species of anuran amphibians (Duellman and Salas, 1991). Of the species of frogs, 54 possess life cycles that include an aquatic tadpole stage.

To insure the presence of tadpoles and to permit consistent sampling and accessibility, the choice of study ponds was based on three general requirements. First, there had to be breeding anurans. Second, the pond had to possess, or exhibit the potential to possess, water for a long enough period of time to allow complete development of at least some tadpole cohorts.
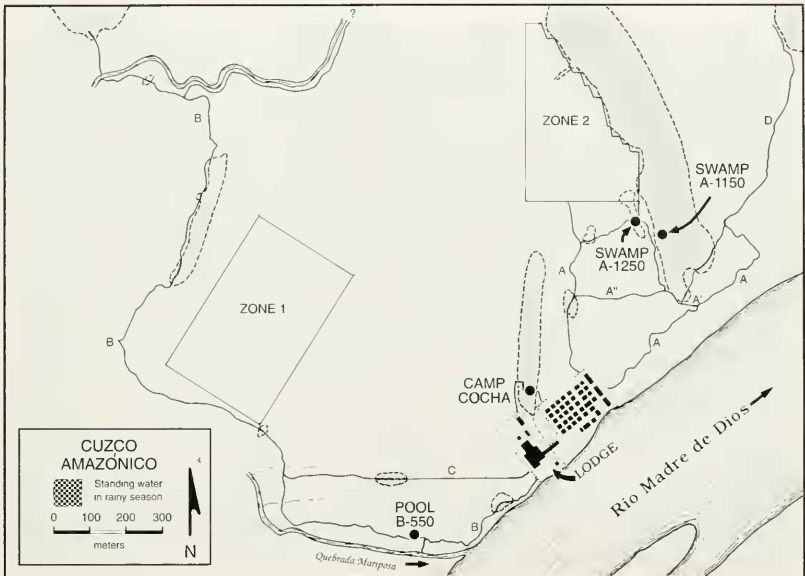
Fig. 1. Map of Cuzco Amazónico showing locations of study ponds: Camp Cocha, Swamp A-1150, Swamp A-1250, and Pool B-550. (Modified from a drawing by Linda Trueb.)

Third, the pond had to be reasonably close to camp and accessible. Some of the ponds initially chosen eventually failed to meet these requirements and proved unsuitable. Four ponds of varied characteristics proved adequate for long-term study (Fig. 1). These are: (1) **Camp Cocha** (Fig. 2)—a permanent *Heliconia* swamp drained by a small creek. This pond is situated 25 m from the edge of the camp clearing, where it creates a large (75×400 m) opening in the terra firma forest canopy. Three 15×1-m transects were cleared for sampling in the center of the south end of the swamp. (2) **Swamp A-1150** (Fig. 3)—a large (150×800 m), permanent swamp in inundated forest. There are few large trees in this swamp and the canopy is incomplete. The understory varies from large open areas to impenetrable dense growths of shrubs and vines. Three 15-m long transects were selected for sampling; these nearly traversed the southern third of the swamp. (3) **Swamp A-1250** (Fig. 4)—a medium-sized (15×100 m), temporarily filled depression in inundated forest. The vegetation resembles at of the adjacent forest with an almost completely enclosed canopy of trees and an understory consisting of scattered shrubs. Three 15-m long transects extending lengthwise down the middle of the swamp were sampled. (4) **Pool B-550** (Fig. 5)—a small (2×5 m), ephemeral pool situated 20 m from the bank of the Quebrada Mariposa. The pool is located in terra firma forest

Fig. 2. The *Heliconia* swamp, Camp Cocha, on 10 March 1990 near the location of the study transects.

Fig. 3. Swamp A-1150 on 10 March 1990 showing site of the sampling transect through the deep pool.

Fig. 4. Swamp A-1250 showing part of sampling transect. (Photo by William E. Duellman, 2 February 1986.)

Fig. 5. Pool B-550 on 11 March 1990.

with an almost completely enclosed canopy and moderately dense under-
brush. Samples were taken from three 1-m long transects across the width
of the pool.

Field Procedures

The sampling regime followed herein is modified from that of Heyer
(1976). Each pond was sampled at three transects with a dipnet near
midday and midnight every second day. Sampling of a transect consisted of
three passes, one each at the surface, the midwater, and the bottom. The
surface usually was sampled first to minimize disturbance of the lower
levels; the sample was made by skimming about the top 10 cm of the water
column. The second and third passes were made midway between the
surface and bottom, and along the bottom, respectively; there was some
overlap in net passes when the water was low. Each of the transects at
Camp Cocha, Swamp A-1150, and Swamp A-1250 was 15 m long. Each
pass consisted of five 3-m sweeps with a pentagonal dipnet (base 40 cm,
sides 21 cm) composed of 5-mm mesh. It became apparent early in the
study it became apparent that smaller tadpoles were not being captured;
therefore, a cheese-cloth covering was sewn inside the coarse mesh to
reduced the mesh size to approximately 1 mm. Because of the smaller size
of Pool B-550 each transect was 1 m long and each pass through a level
could be spanned in a single sweep with a 12×15-cm rectangular net with
mesh of 1 mm. The sampling regime for Pool B-550 differed from that for
other ponds and no attempt was made to standardize volumes sampled or
account for sampling bias.

Tadpoles netted in each sweep were identified, counted, and staged. All
tadpoles were released unless their identity was unknown, in which case
some individuals were preserved as vouchers in 10% buffered formalin
(the method of Altig, 1970), whereas others were reared to identifiable
froglets. Tadpole stage was estimated using the staging table of Gosner
(1960) reproduced in Duellman and Trueb (1986); because of the inaccu-
racy inherent in field-staging, Gosner stages were combined into the fol-
lowing categories: 25, 26–28, 29–31, 32–34, 35–37, 38–40, 41–43. The
data were recorded in the field with a microcassette recorder and later
transcribed into a data book.

Non-anuran organisms (e.g., fish, aquatic insects, and crabs) thought to
be potential predators or competitors, were identified, measured for total
length to the nearest millimeter, and counted. Most of these organisms were
released, although small samples were collected as vouchers and preserved
in 10% buffered formalin for later identification. The preserved tadpoles
and non-anuran organisms were deposited in The University of Kansas
Natural History Museum, and the Museo de Historia Natural at the
Universidad Nacional Mayor de San Marcos in Lima, Peru.

Additional samples were collected frequently in disparate parts of the study ponds to assess the efficacy of the netting procedure in collecting all species present. These additional tadpoles were included in the data analysis only in determining the temporal occurrence of tadpoles. The small size of Pond B-550 permitted a complete and thorough netting at the end of the study period, and all tadpoles were preserved. Ponds other than the four study ponds were visited frequently as potential study sites and to obtain additional specimens to aid in tadpole identification.

A variety of abiotic factors was measured in order to characterize each aquatic habitat and to identify factors influencing tadpole distributions among ponds. Water temperature and depth were recorded at each tadpole sampling. Midwater temperature was measured at each transect and averaged. Water depth was measured with a wooden stake calibrated in centimeters that was permanently installed in the deepest part of each pond near the transects. Thus, the mean depths reported are mean depths at these stakes through time. Light penetration was measured in centimeters during each midday sampling at each depth stake using a Secchi disk. These values are a measure of the amount of the water column receiving sunlight (not turbidity of the water) and are reported as percentages of the depth of the pond. The use of percentages allows relative comparisons of light penetration among ponds of different depths and was necessary because the disk was frequently visible on the bottom in some ponds making comparisons of absolute measurements meaningless (i.e., reporting 25 cm light penetration in two different ponds, one 100 cm deep and another 25 cm deep, hides the fact that the entire water column of the second pond receives light whereas the first pond is only partially illuminated).

Water temperature, pH, dissolved oxygen, hardness, and alkalinity were measured with a Hach™ water-test kit. Water tests were performed initially on samples taken every dawn and dusk in order to detect diel changes in water chemistry. However, late in January a shift was made to every other dawn and dusk (days opposite of tadpole sampling) in order to test all four ponds for the entire season. Water samples were taken from an arbitrarily determined but consistent location near the middle of each study pond. Samples were taken by submerging 500-ml polyethylene bottle to middepth, letting it fill, and capping it underwater so that no air was trapped in the container. The samples were transported to the field laboratory within 1 hr. for completion of the tests. Pond water temperature was measured at midwater coincidentally with water-sample collection.

Daily rainfall was measured with a standard rain gauge located in the camp clearing. To monitor weather fluctuations, ambient air temperature and humidity were recorded continuously throughout the study with a hygrothermograph located in the field laboratory.

Statistical Analyses

Interpond comparisons were made using richness, evenness, and diversity indices. Rarefaction, rather than direct species counts, was used as a richness measure because of unequal sample sizes among ponds (Krebs, 1989). Rarefaction values and their standard deviations were calculated with the program accompanying Krebs (1989). Modified Hill's ratio (Alatalo, 1981) and Hill's numbers were used as evenness and diversity measures, respectively; these calculations were performed with programs accompanying Ludwig and Reynolds (1988). The G-test statistic (Sokal and Rohlf, 1981) was used to test distributions among microhabitats and between diel time periods and was performed with BIOM (Rohlf, 1985). Relationships among the variables of developmental stage, level in the water column, and diel activity of tadpoles were examined by Log-Linear Model Analysis using BMDP (Dixon, 1981) at The University of Kansas Computer Center. Niche breadths were calculated using the measure of Levins (1968), as standardized by Hurlbert (1978), because it is one of the more frequently used niche breadth measures. Niche overlap was calculated using the measure of Morista (1959) because it minimizes bias caused by variation in sample size and number of resource states (Smith and Zaret, 1982). Both of the niche metrics were calculated using modifications of the programs accompanying Krebs (1989).

RESULTS

Natural History

The rainy season of 1989–90 was much drier than the average for the previous 18 yr. (Fig. 6). The average rainfall for December–March was 1355.4 ± 402.6 mm (820.4–2221.1 for 1971–89), whereas the rainfall for these months during 1989–90 was 978.8 mm. The discrepancy between the average rainfall each month and the rainfall for the months of the study period was least in December, when slightly more than average rain fell in 1989–90 (307.0 mm; $\bar{x} = 291.0 \pm 101.1$). The discrepancy between the monthly average and that for the study months increased dramatically during the course of the rainy season, with the greatest difference in March (107.2 mm; $\bar{x} = 287.9$ mm), (Fig. 6). The amount of rain falling in March 1990 was exactly the average amount that falls in May ($\bar{x} = 107.2$ mm); hence, the rainy season was essentially abbreviated by 2 mo.

Although the most rain fell in December, the single 24-hr period with the greatest rainfall was 10 February with 127.6 mm, followed by 28 December with 53.6 mm, 30 January with 49.6 mm, and 13 February with 42.2 mm. Although there were three periods in December with at least three
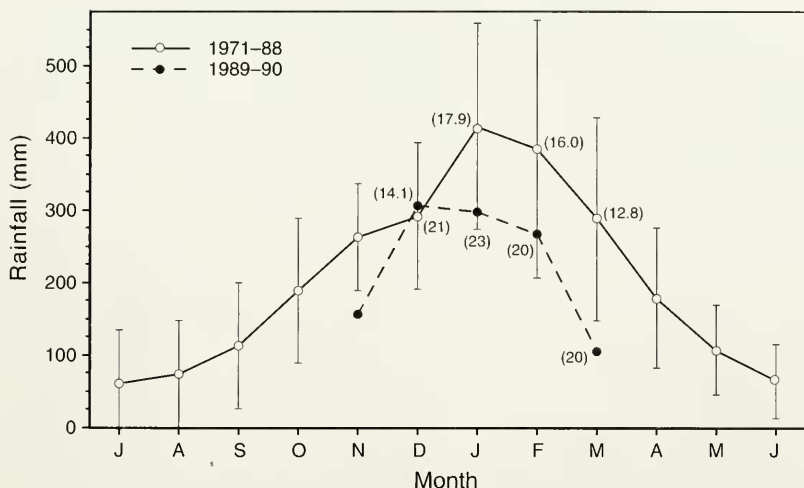
Fig. 6.   Mean monthly rainfall for 1971–1988 at Puerto Maldonado (O) and monthly rainfall for December 1989–March 1990 at Cuzco Amazónico (●). Vertical bars represent ± 1 SD, and the number of days with rain are in parentheses (means for Puerto Maldonado).

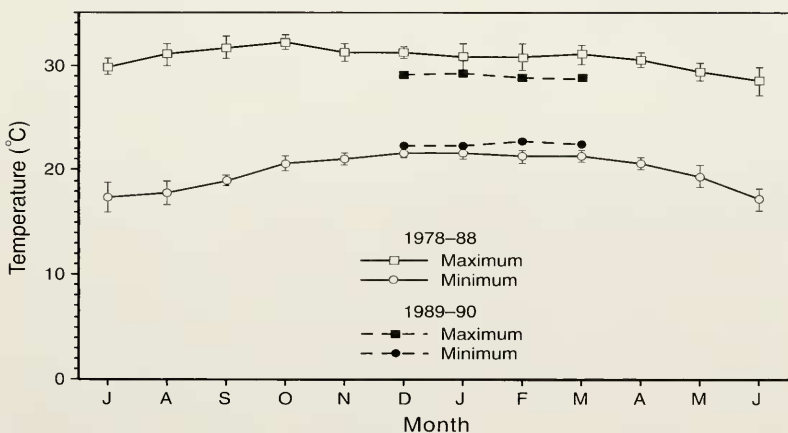Fig. 7.   Monthly mean maximum (▫, ▪) and minimum (O, ●) temperatures for 1978–1988 (averaged over years) at Puerto Maldonado (▫, O) and for December 1989–March 1990 at Cuzco Amazónico (▪, ●).

consecutive days with substantial rain, because these were among the first rains; the water was absorbed quickly by the soil and did not accumulate in ponds. Rainy periods in late January and mid-February seemed to saturate

Table 1.   Summary of tadpoles sampled from the four study ponds.

Species of tadpoles	Camp Cocha	Swamp A-1150	Swamp A-1250	Pool B-550
Dendrobatidae				
Colostethus marchesianus	—	—	1	11
Hylidae				
Hyla brevifrons	1	3	3	—
Hyla fasciata	2	—	—	—
Hyla koechlini	—	1	52	—
Hyla cf. *leali*	—	1	2	6
Hyla leucophyllata	1	12	—	—
Hyla parviceps	—	—	10	38
Hyla sp.	—	2	3	—
Phyllomedusa tomopterna	—	—	—	653
Phyllomedusa vaillanti	2318	55	—	—
Scinax icterica	—	1	299	—
Leptodactylidae				
Leptodactylus mystaceus	—	—	14	—
Microhylidae				
Altigius alios	1	—	—	—
Chiasmocleis ventrimaculata	—	—	109	—
Ctenophryne geayi	—	—	3	—
Elachistocleis ovalis	—	—	38	—
Hamptophryne boliviana	39	3	76	—
Unknown				
Species A	1	—	—	—
Species D	—	—	—	61
Total number of species	7	8	12	5
Total number of tadpoles	2363	78	610	769

the soil, created pools, and raised water levels in the swamps. The number of days with measurable rain was surprisingly higher than average for all months of the study, with January having the most rainy days (Fig. 6). It is possible that this difference is the artificial result of a greater precision of measurement at Cuzco Amazónico or because of a true weather difference between the Reserva Cuzco Amazónico and Puerto Maldonado. Monthly maximum and minimum temperatures were less and greater than average, respectively (Fig. 7).

The known anuran community at Cuzco Amazónico consists of 64 species representing seven families (Duellman and Salas, 1991). Eight species (*Eleutherodactylus* spp. and *Pipa pipa*) have direct development, and two (*Adenomera andreae* and *A. hylaedactyla*) have tadpoles developing in terrestrial foam nests. The remaining 54 species have an aquatic

Table 2.   Summary of non-anuran species sampled from the four study ponds.

Species	Camp Cocha	Swamp A-1150	Swamp A-1250	Pool B-550
Trichodactylidae sp.	187	11	5	10
Belostomatidae				
Belostoma sp.	110	115	1	—
Nepidae sp.	74	102	3	—
Callichthyidae				
Callichthys callichthys	10	11	—	—
Corydoras sp.	—	2	—	—
Characidae				
Species A	—	72	—	—
Species B	—	73	—	—
Species C	—	33	—	—
Cyprinodontidae				
Cynolebias sp.	316	45	1	—
Pterolebias sp.	144	38	—	—
Gasteropelecidae				
Carnegiella sp.	—	38	—	—
Lebiasinidae				
Pyrhulina sp.	4	6	1	—
Species A	—	1	—	—
Total number of species	7	13	5	1
Total number of individuals	845	547	11	10

tadpole stage. A total of 3820 tadpoles of 19 species (35% of the species with tadpoles) representing four families (Dendrobatidae, Hylidae, Leptodactylidae, and Microhylidae) was sampled from the four study ponds throughout the duration of the study (Table 1). Tadpoles of two species (*Hyla allenorum* and *H. fasciata*) that were previously unknown, and a new species of microhylid and its tadpole (*Altigius alios*) are described elsewhere (Wild, 1992, 1995). In addition to the tadpoles, several other organisms that are recognized as potential predators or competitors were encountered in the four study ponds throughout the study period (Table 2), as follows: 213 individuals of one species of crab (Trichodactylidae); 405 individuals of two species of aquatic insects (Nepidae and Belostomatidae); and 795 individuals of 10 species of fish representing five families (Callichthyidae, Characidae, Cyprinodontidae, Gasteropelecidae, and Lebiasinidae). The species of fish include known predatory species (*Callichthys callichthys*, *Cynolebias* sp., *Pterolebias* sp. and *Pryhulina* sp.) that probably feed on tadpoles, but some of the fish species (*Corydoras* sp. and *Carnegiella* sp.) are not predatory at all.
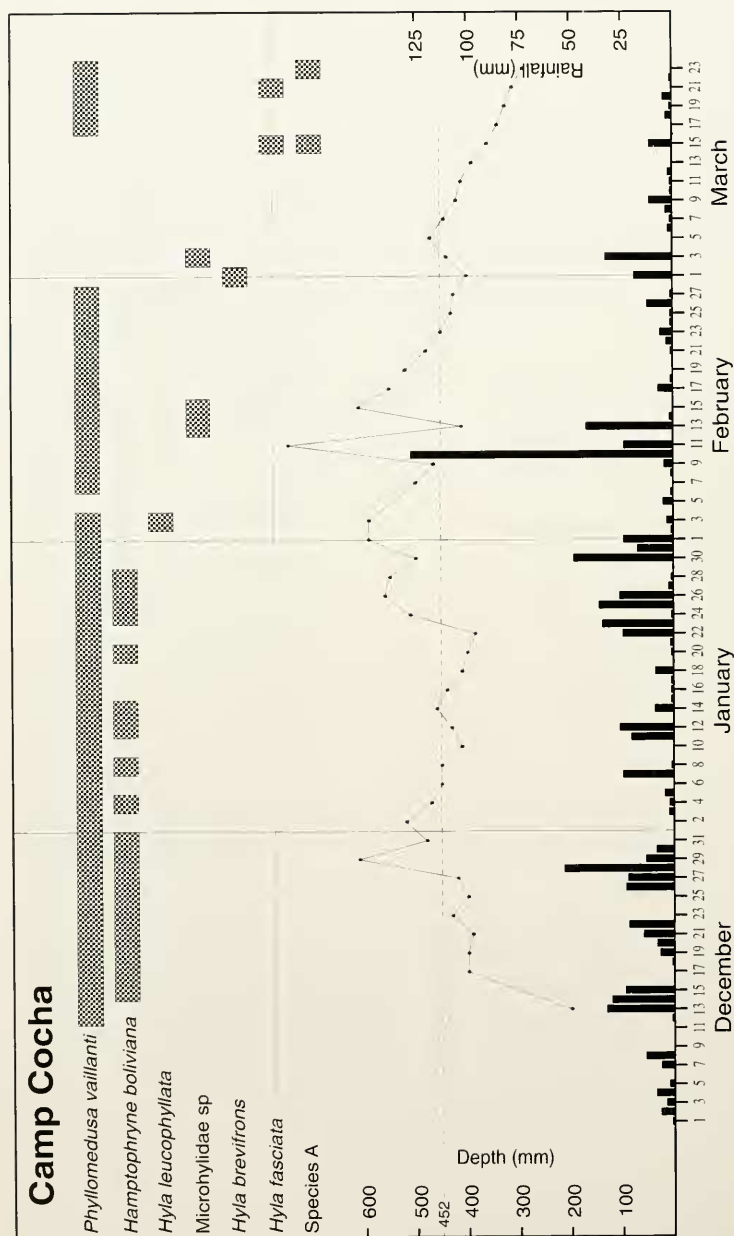
Fig. 8. Temporal occurrence of tadpoles (horizontal bars) and rainfall (vertical bars), and variation in depth (line) of Camp Cocha. Dashed line is mean depth for study period.

Table 3. Abiotic characteristics of the four study ponds. Values for water temperature, dissolved oxygen, pH, alkalinity, and total hardness are given as means ± 1 SD, and for the latter four characteristics the first value is at dusk and the second at dawn.

Characteristics	Camp Cocha	Swamp A-1150	Swamp A-1250	Pool B-550
Width × length (m)	75 × 400	150 × 800	15 × 100	2.3 × 5.2
Depth	452 ± 94	885 ± 178	416 ± 109	144 ± 32
No. days with water	103	104	45	88
Light penetration	76 ± 18%	55 ± 13%	85 ± 21%	90 ± 19%
Water temperature	25.4 ± 0.7	25.1 ± 0.6	25.3 ± 0.6	25.8 ± 1.0
(°C day/night)	25.2 ± 0.8	25.0 ± 0.7	25.4 ± 0.6	25.4 ± 0.9
Dissolved oxygen	6 ± 1	7 ± 1	6 ± 1	7 ± 1
(mg/l)	6 ± 1	6 ± 1	7 ± 1	7 ± 1
pH	6.5 ± 0.1	6.6 ± 0.2	6.7 ± 0.3	6.6 ± 0.2
	6.5 ± 0.1	6.5 ± 0.2	6.7 ± 0.3	6.7 ± 0.3
Alkalinity	37 ± 9	30 ± 8	63 ± 21	43 ± 18
(mg/l CaCO3)	42 ± 8	30 ± 7	64 ± 17	48 ± 16
Total hardness	49 ± 10	42 ± 10	68 ± 17	49 ± 12
(mg/l Ca CO3)	56 ± 12	41 ± 12	73 ± 14	53 ± 19

CHARACTERISTICS OF STUDY PONDS

Camp Cocha.—*Abiotic characteristics (Table 3):* Camp Cocha is a large *Heliconia* (Musaceae) swamp situated 25 m from the camp clearing where it creates a large opening in the canopy of terra firma forest. The swamp supports a dense growth of *Heliconia* and a few low shrubs. Although there are few living trees in the swamp there are numerous dead trunks in the water. The swamp is drained by a small creek at the southern end that varied in flow from totally dry to a rushing torrent after heavy rains. Standing water was present for the entire 103 days of the study period (11 December 1989–23 March 1990). Although the swamp is permanent, observations during July 1989, when there were only shallow puddles of standing water, indicate that water is reduced substantially during the dry season. During the rainy season of 1990, the swamp filled to a maximum size of about 75 × 400 m. The mean water depth throughout the study period was 452 ± 94 mm; the shallowest depth was 200 mm on 13 December (the first day of sampling) and the greatest depth was 750 mm on 11 February (the day after the heaviest rainfall). Water temperature varied little between day ($\bar{x}$ = 25.4 ± 0.7°C) and night ($\bar{x}$ = 25.2 ± 0.8°C), and throughout the study period varied from 23.0–27.0°C. The mean depth of light penetration during the study period was 76 ± 18% of the water column. Light penetrated to the bottom (100%) on 11 days and penetrated less than 50% of the depth only once (48%).

Table 4.   Species with adults (A), tadpoles (T), or both (B) encountered at the four study ponds.

Species	Camp Cocha	Swamp A-1150	Swamp A-1250	Pool B-550
Bufonidae				
Bufo marinus	A	—	—	—
Dendrobatidae				
Colostethus marchesianus	—	—	B	B
Hylidae				
Hyla allenorum	A	—	—	—
Hyla brevifrons	B	B	T	—
Hyla fasciata	B	A	A	—
Hyla koechlini	A	T	B	—
Hyla cf. *leali*	—	T	B	B
Hyla leucophyllata	B	B	—	—
Hyla parviceps	—	A	B	B
Hyla schubarti	A	—	—	—
Hyla sp.	—	T	T	—
Osteocephalus taurinus	—	A	—	A
Phyllomedusa tomopterna	—	—	—	B
Phyllomedusa vaillanti	B	B	—	—
Scarthyla ostinodactyla	A	A	A	—
Scinax garbei	A	—	—	—
Scinax icterica	—	B	B	—
Sphaenorhynchus lacteus	A	—	—	—
Leptodactylidae				
Ceratophrys cornuta	—	—	A	—
Leptodactylus leptodactyloides	—	—	A	—
Leptodactylus mystaceus	—	—	T	—
Leptodactylus petersii	A	A	—	—
Microhylidae				
Altigius alios	T	—	—	—
Chiasmocleis ventrimaculata	—	—	B	—
Ctenophryne geayi	—	—	B	—
Elachistocleis ovalis	—	—	T	—
Hamptophryne boliviana	T	T	B	—
Unknown				
Species A	T	—	—	—
Species D	—	—	—	T
Total number of species present only as adults (A)	8	5	4	1
Total number of species present only as tadpoles (T)	3	4	4	1
Total number of species present as adults and tadpoles (B)	4	4	8	4

The mean dissolved oxygen content of the water was constant between dawn and dusk ($\bar{x} = 6 \pm 1$ mg/l) but varied from 4–10 mg/l at dusk 29 December and 11 March, respectively. The water pH varied little throughout the study and was consistent from dawn to dusk ($\bar{x} = 6.5 \pm 0.1$). The mean alkalinity was slightly higher at dawn ($\bar{x} = 42 \pm 8$ mg/l) than dusk ($\bar{x} = 37 \pm 9$ mg/l), and reached extremes of 20 and 72 mg/l at dusk 06 January and dawn 16 March, respectively. The mean total hardness was slightly higher at dawn ($\bar{x} = 56 \pm 12$) than at dusk ($\bar{x} = 49 \pm 10$) and reached extremes of 20 and 90 mg/l at dusk 11 February and dawn 16 March, respectively.

Biotic characteristics: Throughout the study period, 2363 tadpoles of seven species were sampled from Camp Cocha (Table 1). Ninety-eight percent of these were *Phyllomedusa vaillanti* ($n = 2318$), followed by the microhylid *Hamptophryne boliviana* with 2% ($n = 39$). The remaining five species ($n = 6$) were collected only rarely (*Hyla fasciata* twice, the others only once each). Casual observations of adult anurans present near the pond indicate that the tadpoles do not represent the same species. This may indicate an inefficient sampling technique, but this disparity between the local adult community and an associated tadpole assemblage has been documented elsewhere (Dixon and Heyer, 1968; Heyer, 1973; Gascon, 1991). Furthermore, additional netting in disparate parts of the study ponds rarely produced species not found in the sampling transects. These few additional tadpoles were included in the data analysis only in determining the temporal occurrence of tadpoles. Adults, but no tadpoles, of the following species were present: *Bufo marinus, Hyla allenorum, H. koechlini, H. schubarti, Leptodactylus petersii, Scarthyla ostinodactyla, Scinax garbei,* and *Sphaenorhynchus lacteus* (Table 4). Although tadpoles of *H. boliviana* and *Altigius alios* were found, no adults were observed. One tadpole, Species A, could not be identified. Tadpoles were present for essentially the entire study period (Fig. 8). Tadpoles of *P. vaillanti* were taken on the first (13 December) and last (23 March) days of sampling as well as most days in between. Apparently these represent the product of three breeding bouts, the tadpoles of which demonstrate synchronous development; the first bout started prior to 13 December, another around 03 February, and the third prior to 15 March. Tadpoles of *Hamptophryne boliviana* were first collected on 15 December, after the first of two breeding bouts, the second being around 2 January; *H. boliviana* tadpoles were not found after 28 January. Tadpoles of each of the remaining species were the result of a single breeding bout and were encountered at various times throughout February and March, but mostly after the heaviest rainfall on 10 February.

Seven non-anuran species were collected in net samples from Camp Cocha, as follows: 187 individuals of the trichodactylid crab species; 184 of the two species of insects; and 474 of seven species of fish (Table 2). All of these, except the fishes *Callichthys callichthys* and *Pyrhulina* sp., were present throughout the study period.

Swamp A-1150.—*Abiotic characteristics (Table 3):* Swamp A-1150 is a large, permanent swamp in inundated forest. Few large trees are present, and the canopy is incomplete. The understory varies from wide, open areas to impenetrable dense growths of shrubs and vines. The presence of a small (3 × 5 m) pool about 0.5 m deep in July 1989 indicates that at least part of the swamp contains standing water throughout the year. Standing water was present for the entire 104 days of the study period (11 December 1989–24 March 1990). During the rainy season of 1990 the swamp reached a maximum size of about 150 × 800 m. The mean water depth throughout the study period was 885 ± 178 mm. The shallowest depth recorded at this location was 610 mm on 24 March, the last visit, whereas the greatest depth was 1375 mm on 12 February, 2 days after the heaviest rainfall. Water temperature varied little between day ($\bar{x} = 25.1 \pm 0.6°C$) and night ($\bar{x} = 25.0 \pm 0.7°C$) or throughout the study period (23.0–26.5°C). The mean depth of light penetration was 55 ± 13% of the water column. The greatest percentage of depth that light penetrated was 89%. Light penetrated less than 50% of the water depth on 18 days, and the least penetration was 20%.

The mean dissolved oxygen content of the water of Swamp A-1150 did not vary significantly between dawn ($\bar{x} = 6 \pm 1$ mg/l) and dusk ($\bar{x} = 7 \pm 1$ mg/l), and reached extremes of 4 and 11 mg/l at dawn 16 December and dusk 16 March, respectively. The water pH varied little throughout the study and between dawn ($\bar{x} = 6.5 \pm 0.2$) and dusk ($\bar{x} = 6.6 \pm 0.2$), and reached extremes of 6.0 and 7.0. The mean alkalinity was nearly identical at dawn ($\bar{x} = 30 \pm 7$) and dusk ($\bar{x} = 30 \pm 8$), and reached extremes of 14 and 46 mg/l at dawn on 12 and 21 December, respectively. The mean total hardness was nearly the same at dawn ($\bar{x} = 41 \pm 12$) and dusk ($\bar{x} = 42 \pm 10$) and reached extremes of 20 and 60 mg/l on several occasions.

Biotic characteristics: During the study period 78 tadpoles of 8 species were sampled from Swamp A-1150 (Table 1). Seventy-one percent ($n = 55$) were *Phyllomedusa vaillanti* and 15% ($n = 12$) were *Hyla leucophyllata*. The remaining six species ($n = 11$) were only taken rarely. Casual observations of adults present at the site indicates that there were fewer species of anuran larva than adults. Adult *Hyla fasciata, H. parviceps, Leptodactylus petersii, Osteocephalus taurinus,* and *Scarthyla ostinodactyla* were present, but tadpoles of none of these were collected (Table 4). Although tadpoles of *Hamptophryne boliviana, Hyla koechlini,* and *H.* cf. *leali* were collected, no adults were seen. One tadpole, *Hyla* sp., could not be identified. Tadpoles were not present for the entire study period (Fig. 9). Tadpoles of *H. boliviana* were the first encountered on 13 January and none was collected after 08 February. *Phyllomedusa vaillanti* larvae were taken on 15 and 17 January, but not again until 18 February; apparently these were the result of two separate breeding bouts. *Hyla leucophyllata* was collected periodically between 08 February and 14 March, and *H. brevifrons* was found once on
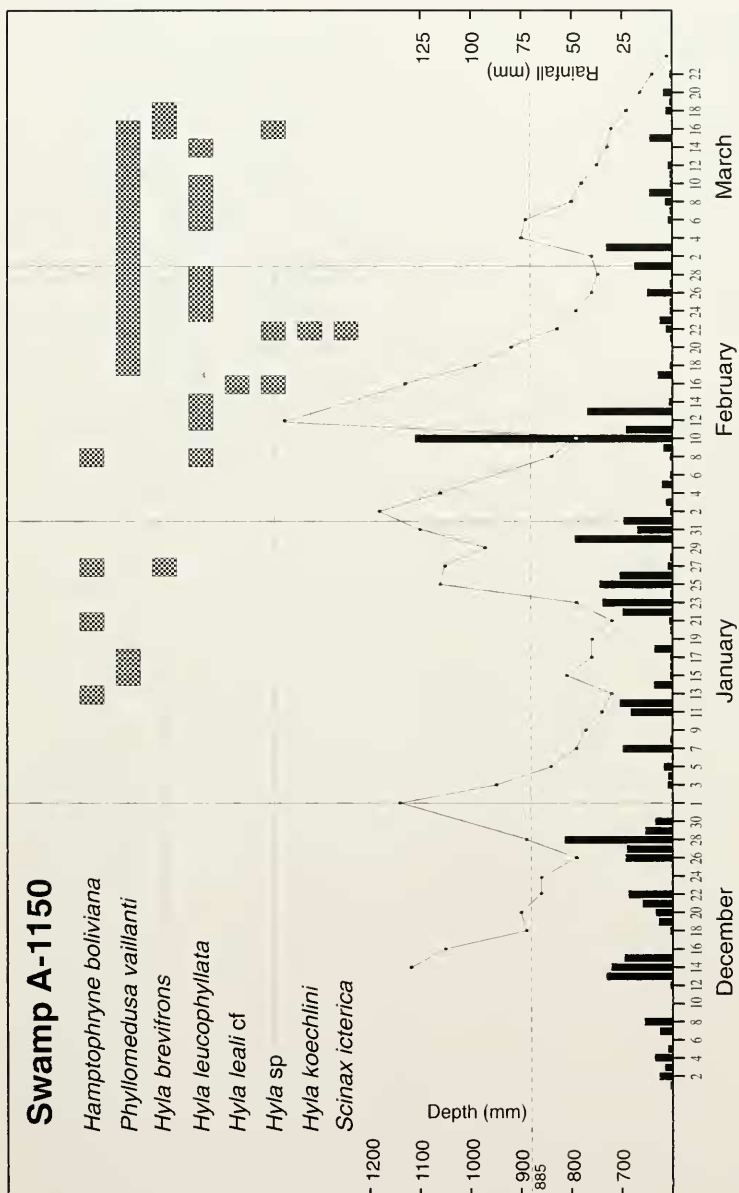
Fig. 9. Temporal occurrence of tadpoles (horizontal bars) and rainfall (vertical bars), and variation in depth (line) of Swamp A-1150. Dashed line is mean depth for study period.

27 January and not again until 16 March. *Hyla koechlini, H.* cf. *leali, H.* sp., and *Scinax icterica* were encountered only after the heavy rainfall of 10 February.

Thirteen non-anuran species were collected in Swamp A-1150, as follows: 11 individuals of the trichodactylid crab species; 217 of the two species of insect; and 319 of 10 species of fish (Table 2). The crab was present primarily during the first half of the study period (December–January). Both insect species were present throughout the study. Of the fish, *Carnegiella* sp., *Characidae* sp. A, and *Cynolebias* sp., were collected throughout the study period, whereas *Callichthys callichthys*, Characidae sp. B, and *Pterolebias* sp. were taken primarily during the first half. Characidae sp. C was found only throughout January and February, whereas *Coryduras* sp., *Pyrhulina* sp., and Species A rarely were encountered. In addition, two colubrid snakes were found—one *Chironius fuscus* on vegetation above the water, and one *Clelia clelia* in the water.

Swamp A-1250.—*Abiotic characteristics (Table 3):* Swamp A-1250 is a temporarily filled depression in the inundated forest floor. The vegetation of the swamp is similar to that of the adjacent forest; the canopy is almost completely closed and the understory consists of scattered shrubs. The depression was dry in July 1989, indicating that Swamp A-1250 is temporary. Water was noted on 29 December; although the water had decreased in depth, it was 280 mm deep on 01 January. The water level dropped so rapidly that on 02 January, much of the transect consisted of only wet leaf litter. Only footprints in the mud held water until 23 January, when the swamp filled and maintained standing water for 45 days until 08 March. The mean water depth during this period was 416 ± 109 mm. The maximum depth at this location of 580 mm occurred on 14 February when the swamp reached a size of about 20×100 m. Water temperature varied little between day ($\bar{x} = 25.3 \pm 0.6°C$) and night ($\bar{x} = 25.4 \pm 0.6°C$) and ranged from 24–26°C. The mean light penetration over the study period was $85 \pm 21\%$ of the water column; light penetrated to the bottom (100%) frequently, and the least light penetration was 53%.

The dissolved oxygen content of the water of Swamp A-1250 did not vary significantly between dawn ($\bar{x} = 7 \pm 1$ mg/l) and dusk ($\bar{x} = 6 \pm 1$ mg/l), and reached extremes of 5 and 10 mg/l at dusk on 30 January and 05 March, respectively. The mean water pH was identical at dusk and dawn ($\bar{x} = 6.7 \pm 0.3$) and varied little throughout the study period (6.5 – 7.0). The water alkalinity differed little between dawn ($\bar{x} = 64 \pm 17$ mg/l) and dusk ($\bar{x} = 63 \pm 21$ mg/l), and reached extremes of 30 and 92 mg/l. Total hardness was slightly higher at dawn ($\bar{x} = 73 \pm 14$ mg/l) than at dusk ($\bar{x} = 68 \pm 17$ mg/l), and reached extremes of 50 and 90 mg/l on several occasions.

Biotic characteristics: Throughout the study period 610 tadpoles of 12 species were sampled from Swamp A-1250 (Table 1). *Scinax icterica* (49%, $n = 299$) was the most abundant species, followed by *Chiasmocleis*
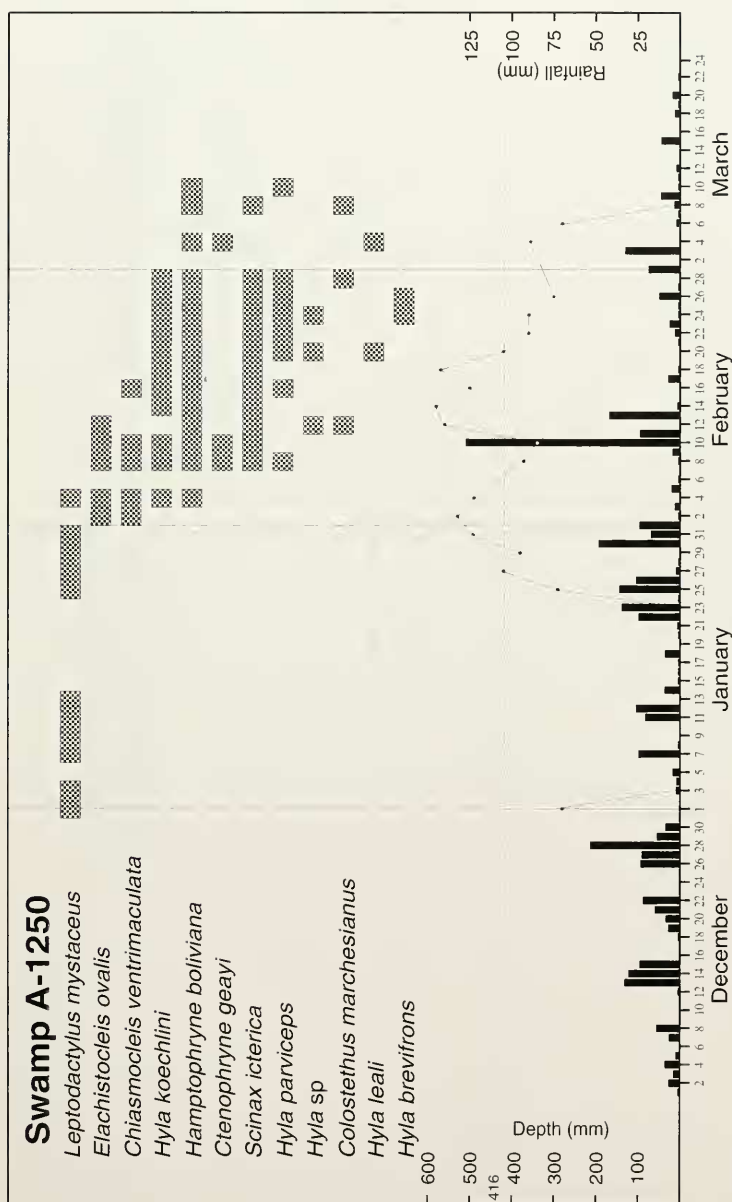
Fig. 10. Temporal occurrence of tadpoles (horizontal bars) and rainfall (vertical bars), and variation in depth (line) of Swamp A-1250. Dashed line is mean depth for study period.

ventrimaculata (18%, n = 109), *Hamptophryne boliviana* (12%, n = 76),
Hyla koechlini (9%, n = 52), and *Elachistocleis ovalis* (6%, n = 38). Other
species that were collected rarely and accounted for 6% (n = 36) are
Colostethus marchesianus, Ctenophryne geayi, Hyla brevifrons, H. cf.
leali, H. parviceps, H. sp., and *Leptodactylus mystaceus.* Adult *Ceratophrys
cornuta, Leptodactylus leptodactyloides, Scarthyla ostinodactyla,* and *Hyla
fasciata* were present, but no larvae of these species were collected (Table
4). Although tadpoles of *Elachistocleis ovalis, Hyla brevifrons,* and
Leptodactylus mystaceus were found, no adults were seen in the vicinity.
One tadpole, *Hyla* sp., could not be identified. Adults of *Hyla leali* and *H.
rhodopepla* were present, but their tadpoles are indistinguishable; thus, the
tadpole referred to as *H.* cf. *leali* could be either or both of these taxa. A
large chorus on the night of 25 January when *Ctenophryne geayi,
Ceratophrys cornuta, Hamptophryne boliviana, Hyla koechlini, H.
parviceps, Leptodactylus leptodactyloides,* and *Scinax icterica* were active
seems to have signaled the initial and primary breeding activity that led to
the tadpole fauna in Swamp A-1250. Prior to February, only *Leptodactylus
mystaceus* larvae were encountered, but by 08 February, all of the afore-
mentioned species of the chorus, except *Ceratophrys cornuta* and
Leptodactylus leptodactyloides, were present as tadpoles in addition to
Chiasmocleis ventrimaculata and *Elachistocleis ovalis.* There were subse-
quent choruses but none of the magnitude of the first one. Tadpoles were
found whenever water was present (Fig. 10). The first tadpoles that ap-
peared were *Leptodactylus mystaceus* on 01 January; these were the only
anuran larvae present prior to February and they were absent after 04
February. It seems as though tadpoles of *L. mystaceus* resulted from two
breeding bouts, because young tadpoles were present on 01 January and
again on 25 January; all other species seem to have resulted from a single
breeding bout. *Chiasmocleis ventrimaculata, Ctenophryne geayi,
Elachistocleis ovalis, Hamptophryne boliviana, Hyla koechlini, H.
parviceps,* and *Scinax icterica* all appeared in net samples in the first week
of February. *Colostethus marchesianus, Hyla brevifrons, H.* cf. *leali,* and
Hyla sp. appeared later; the latest was *H. brevifrons* on 24 February. Only
Colostethus marchesianus, Hamptophryne boliviana, Hyla parviceps, and
Scinax icterica were collected in March; the last species encountered were
H. boliviana and *H. parviceps* on 08 March.

     Five non-anuran species were collected in net samples of Swamp A-
1250, as follows: five individuals of the trichodactylid crab species; three
individuals of Nepidae sp.; and one each of *Belostoma* sp., *Cynolebias* sp.,
and *Pyrhulina* sp. (Table 2). The crab was found only in late January,
whereas the remaining non-anuran species were encountered between 14 –
24 February. Two colubrid snakes (*Liophis reginae, Helicops* sp.), a chelid
turtle (*Platemys platycephala*), and a crocodylid (*Paleosuchus trigonatus*)
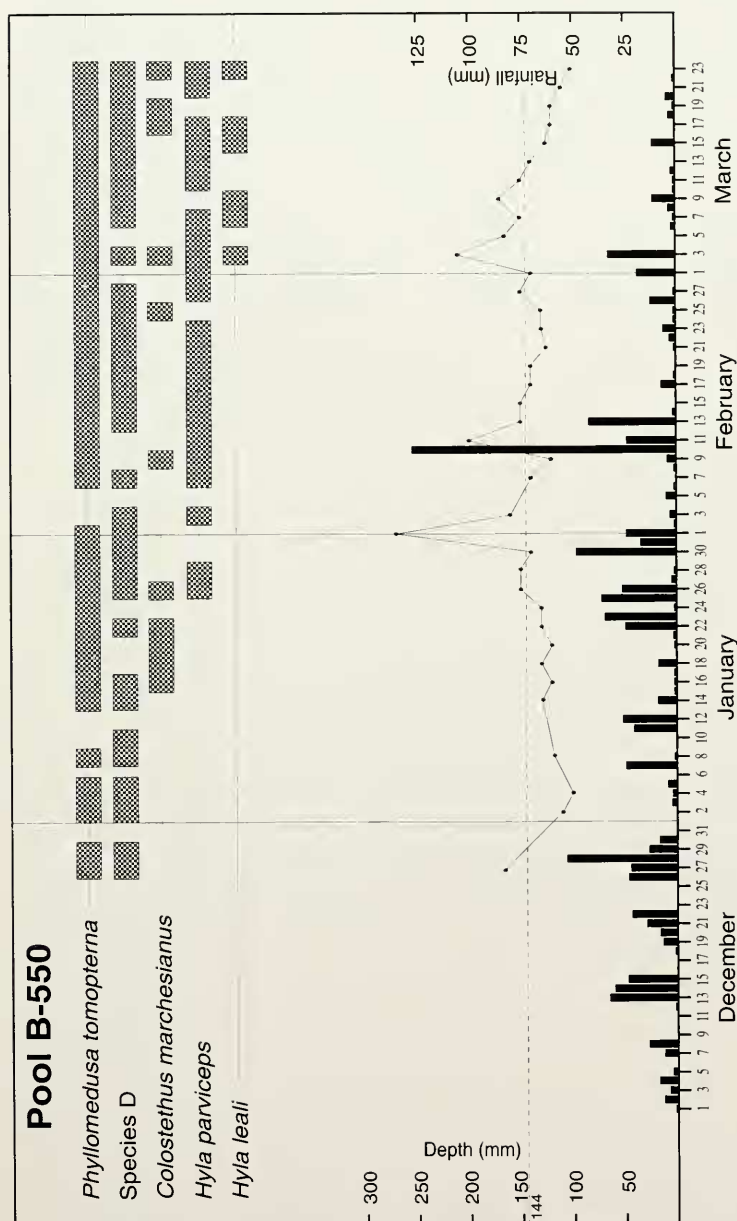also were found in Swamp A-1250.

Fig. 11. Temporal occurrence of tadpoles (horizontal bars) and rainfall (vertical bars), and variation in depth (line) of Pool B-550. Dashed line is mean depth for study period.

Pool B-550.—*Abiotic characteristics (Table 3):* Pool B-550 is a small, ephemeral pool situated 20 m from the bank of the Quebrada Mariposa. The pool is located in terra firma forest with an almost completely closed canopy and moderately dense understory of vines and many shrubs. Pool B-550 began to fill a few days prior to 27 December, the date sampling started, and contained standing water until sampling was terminated on 23 March (88 days). The mean water depth during this time was 144 ± 32 mm; the water depth reached a maximum of 270 mm on 01 February and was never less than 100 mm. At its average depth, the pool was 2.3×5.2 m, and at its greatest depth, 2.6×6.5 m. Prior to late December, there was no indication that this pool existed other than a slight depression in the forest floor. Water temperature varied little between day ($\bar{x} = 25.8 \pm 1.0°C$) and night ($\bar{x} = 25.4 \pm 0.9°C$) and reached extremes of 23 and 27°C. Because of the shallowness of the pool, light penetrated to the bottom most of the time, and was less than 70% of the water column only once (38%).

The dissolved oxygen content of the water in Pool B-550 was the same at dawn and dusk ($\bar{x} = 7 \pm 1$ mg/l), and reached extremes of 5 and 10 mg/l at dusk 31 January and 03 March, respectively. The mean water pH varied little between dawn ($\bar{x} = 6.7 \pm 0.3$) and dusk ($\bar{x} = 6.6 \pm 0.2$), and reached extremes of 6.5 and 7.0. The mean water alkalinity was slightly higher at dawn ($\bar{x} = 48 \pm 16$) than at dusk ($\bar{x} = 43 \pm 18$) and reached extremes of 18 and 88 at dusk on 11 February and dawn 20 March, respectively. Total hardness was slightly higher at dawn ($\bar{x} = 53 \pm 9$) than dusk ($\bar{x} = 49 \pm 12$), and reached extremes of 30 and 100, the first on several occasions and the second at dawn on 20 March.

Biotic characteristics: Throughout the study, 769 tadpoles of five species were sampled from Pool B-550 (Table 1). *Phyllomedusa tomopterna* was the most abundant species with 85% ($n = 653$) of all tadpoles sampled, followed by Species D with 8% ($n = 61$). *Hyla parviceps* ($n = 38$), *Colostethus marchesianus* ($n = 11$), and *Hyla* cf. *leali* ($n = 6$) accounted for the remaining 7%. Adults of all species, except for the unknown Species D, were present or heard calling near Pool B-550 at some time during the study (Table 4). The most frequently encountered adults were *Hyla parviceps* and *Phyllomedusa tomopterna.* Tadpoles were present for the entire sampling period (Fig. 11). *Phyllomedusa tomopterna* and Species D were the only species present for the entire period; because these larvae were present on the first day of sampling, breeding must have occurred previously. On 14 January, there was an additional hatching of *Phyllomedusa tomopterna* that resulted in the presence of smaller tadpoles and individual eggs in the water. On 24 January, there were two size classes of *P. tomopterna* larvae present; the presence of young tadpoles indicates an additional hatching. Larvae of Species D seemed to have resulted from three additional hatchings; one in mid-January, another in mid-February,

and the third in early March. *Colostethus marchesianus* was found first on 16 January, and subsequently, was encountered infrequently. *Hyla parviceps* was present from 26 January until 23 March, and *H.* cf. *leali* was present only in March. Tadpoles of all species, except *H.* cf. *leali,* plus an additional unknown Species A, were present when the entire tadpole fauna was removed by thorough netting on 23 March. The abundances of the tadpoles of this final netting were: *Phyllomedusa tomopterna*—32, Species D—31, *Colostethus marchesianus*—26, *Hyla parviceps*—22, and Species A—5.

The only non-anuran species sampled from Pool B-550 was the species of trichodactylid crab (Table 2). Crabs were first found on 16 January and were occasionally taken thereafter until 19 March. A chelid turtle (*Phrynops gibbus*) and a colubrid snake (*Helicops polylepis*) were also encountered at Pool B-550.

COMPARISONS OF STUDY PONDS

Abiotic Factors (Table 3).—The study ponds differed markedly in vegetation, pond structure, permanency, size, and depth. Camp Cocha and Pool B-550 were both located in terra firma forest; however, they differed in many respects, including vegetation. Camp Cocha was densely vegetated, almost exclusively by *Heliconia*, creating a large opening in the forest canopy. Thus, it was distinct from the surrounding forest. The vegetation of the small Pool B-550 resembled that of the surrounding forest, having a moderately dense underbrush of vines and woody shrubs under an almost completely closed canopy. In the dry season, Pool B-550 was virtually undetectable because it was simply a slightly depressed area in the forest floor, whereas Camp Cocha remained distinct from the surrounding forest throughout the annual cycle.

Swamps A-1150 and A-1250 covered large areas in the inundated forest. These swamps were only 100 m apart, and the forest surrounding them was similar. However, the vegetational composition of these two swamps was quite different. The forest canopy over swamp A-1150 was incomplete, and the understory varied from wide, open areas to impenetrable, dense growths of woody shrubs and vines. Swamp A-1250, in contrast, had an almost completely closed canopy, like that of the surrounding forest, and the sparse understory consisted only of scattered woody shrubs. Both swamps had downed trunks, smaller branches, and vines in the water.

The permanency of study ponds differed. Both Camp Cocha and Swamp A-1150 contained standing water throughout the study period. Swamp A-1150 contained standing water during the dry season, but Camp Cocha did not although the ground remained wet. Pool B-550 was temporary; after the first several consecutive days of rain and ground saturation, the pond maintained a relatively constant level of standing water. The temporary

Swamp A-1250 was the most ephemeral and required several days of rain to fill and maintain a constant level of standing water; in the absence of rain, the water level dropped and the swamp dried rapidly. The relative sizes and depths of the ponds does not perfectly corresponded to their permanency. Whereas Swamp A-1150 was the largest, deepest, and most permanent, followed by Camp Cocha, Pool B-550 was the smallest and shallowest yet less ephemeral than the larger, deeper Swamp A-1250.

Pool B-550 had the greatest mean percentage light penetration followed by Swamp A-1250 and Camp Cocha. Swamp A-1150 had a much lower average amount of light penetration than the other three ponds. The amount of light penetration is related to water depth and simply reflects the presence or absence of an unlit zone.

There was relatively little difference in the water chemistry of the ponds. All had similar water temperatures, dissolved oxygen contents, and pHs, all of which showed little diel variation throughout the study as well. Water alkalinity was lower in Swamp A-1150 than in the other study ponds, and highest in Swamp A-1250. All ponds had slightly higher alkalinity at dawn than at dusk, except Swamp A-1150, in which alkalinity was nearly constant. A similar diel pattern was found for total water hardness. Among ponds, total hardness, like alkalinity, was the lowest in Swamp A-1150 and the highest in Swamp A-1250. Total hardness was slightly higher at dawn than at dusk for all study ponds except A-1150, in which hardness was nearly constant.

In summary of abiotic characteristics, each study pond had different vegetation and structure. There was a continuum of permanency, size, and depth among the ponds. Thus, Swamp A-1150 was the most permanent, largest, and deepest pond followed by Camp Cocha in all three aspects. Swamp A-1250 was larger and deeper than Pool B-550, but was more ephemeral. Percentage light penetration was inversely related to size and depth of the ponds. The ponds were similar in water temperature, dissolved oxygen content, and pH, and showed no diel shifts in these abiotic factors. Alkalinity and total hardness were inversely related to pond permanency. All of the study ponds except A-1150 showed a slight diel shift, with both alkalinity and total hardness being higher at dawn.

Biotic Comparisons.—The greatest number of tadpoles yielded by any pond was 2363 from Camp Cocha. Pool B-550, Swamp A-1250, and Swamp A-1150 followed with 769, 610, and 78 tadpoles, respectively. In terms of the number of species, Swamp A-1250, with 12, was the richest, followed by Swamp A-1150, Camp Cocha, and Pool B-550 with eight, seven, and five species, respectively. When sampling effort, reflected in the total number of tadpoles sampled in each pond, is taken into account by using rarefaction for samples of equal sample sizes ($n = 78$), Swamp A-1150 is the richest (8.00 ± 0.00), followed by Swamp A-1250 (7.98 ± 1.12),

Pool B-550 (4.15 ± 0.69) and Camp Cocha (1.93 ± 0.62), (Fig. 12). The low values in Camp Cocha and Pool B-550 reflect the predominance of one common species and several rare species. This is better illustrated using modified Hill's ratio for measuring evenness (Table 5). Camp Cocha (E = 0.35) is the least equitable followed by Pool B-550 (E = 0.46), and Swamp A-1150 (E = 0.50), whereas Swamp A-1250 is the most equitable (E = 0.62). Diversity measured by Hill's numbers combines both evenness and species richness into a measure of the effective number of abundant (N1) and very abundant (N2) species. Camp Cocha (N2 = 1.04) clearly has a single dominant species, *Phyllomedusa vaillanti,* and few abundant species (N1 = 1.11), indicating that most species are very rare. Pool B-550 has a slightly higher value for very abundant species (N2 = 1.37), but it is also close to one, with *Phyllomedusa tomopterna* being the primary species. Compared to Camp Cocha, Pool B-550 has more abundant species (N1 = 1.80). Both Swamps A-1150 and A-1250 have a greater number of very abundant (N2 = 1.93 and 3.35, respectively), as well as abundant species (N1 = 2.85 and 4.76, respectively).

Pairwise comparisons of the ponds indicated that Swamps A-1150 and A-1250, the two ponds nearest each other, had the greatest number of species of tadpoles in common, with six shared species (and the second greatest in number of species as adults). This pair is followed by Swamp A-1150 and Camp Cocha, the third most proximate pair, with four shared species of tadpoles (and the greatest number of adults in common). Pool B-550 had three species in common with Swamp A-1250, one species in
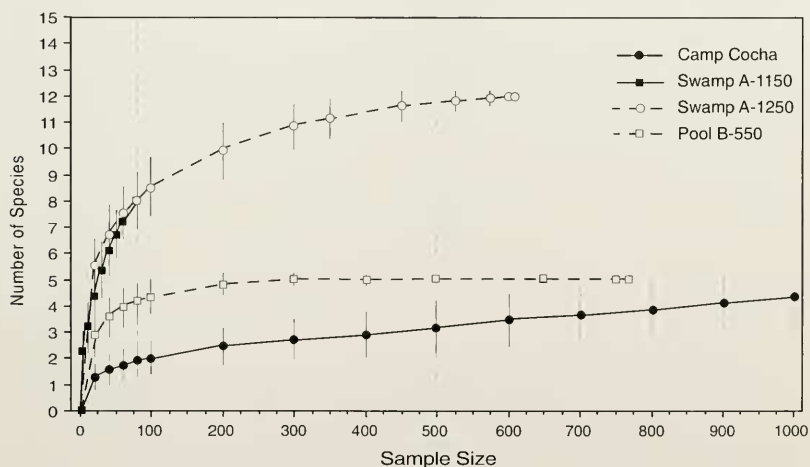

Fig. 12. Rarefaction curves for tadpole species of the four study ponds. Error bars = ± 1SD and vertical dashed lines indicate sample sizes of 78 (left) and 500 (right) individuals.

Table 5.   Tadpole species richness, abundance, evenness, and diversity in the four study ponds.

Pond	No. of species	No. of tadpoles	Rarefaction ($n = 78$)	Evenness (E)	Diversity (N1)	(N2)
Camp Cocha	7	2363	1.93 ± 0.62	0.35	1.11	1.04
Swamp A-1150	8	78	8.00 ± 0.00	0.50	2.85	1.93
Swamp A-1250	12	610	7.98 ± 1.12	0.62	4.76	3.35
Pool B-550	5	769	4.15 ± 0.69	0.46	1.80	1.37
Total	19	3820				

common with Swamp A-1150, but none with Camp Cocha, even though these were the second most proximate pair. Camp Cocha and Swamp A-1150 had two species of tadpoles in common. Swamp A-1150 and Camp Cocha had the greatest number of species of adults in common with six, followed by Swamps A-1150 and A-1250 with four. Swamp A-1250 had three species of adults in common with Camp Cocha and Pool B-550. Pool B-550 and Swamp A-1150 had two species in common, whereas Camp Cocha and Pool B-550 had none, in spite of their being the most proximal pair.

The greatest number of non-anurans yielded by any pond was 845 from Camp Cocha. Swamps A-1150 and A-1250, and Pool B-550 followed with 547, 11, and 10 individuals, respectively. In terms of only the number of species, Swamp A-1150, with 13, was the richest followed by Camp Cocha, Swamp A-1250, and Pool B-550 with seven, five, and one respectively. The only non-anuran species found in Pool B-550 was the single species of crab, which was encountered rarely. Taking into account sampling effort (number of individuals sampled), rarefaction ($n = 10$) indicated Swamp A-1150 to be the richest in non-anuran species (5.91 ± 1.05) followed by Swamp A-1250 (5.00 ± 0.00) and Camp Cocha (4.27 ± 0.79), (Fig. 13). The evenness measure of modified Hill's ratio shows Camp Cocha to be the least equitable in non-anuran abundance (E = 0.83), followed closely by Swamp A-1150 (E = 0.85); (Table 6). Swamp A-1250 was the most equitable in non-anurans (E = 1.10). Only Pool B-550 was dominated by one non-anuran species, the crab, which was the only species present and very rare. All other three ponds had approximately equivalent numbers of very abundant and abundant species of non-anurans. Swamp A-1150 had the greatest of both (N1 = 8.68, N2 = 7.49), followed by Camp Cocha (N1 = 4.76, N2 = 4.17). Swamp A-1250 had more very abundant (N2 = 4.23) than abundant (N1 = 3.92) species.

Pairwise comparisons of non-anuran species among the study ponds showed that Camp Cocha and Swamp A-1150 had the greatest number (7)
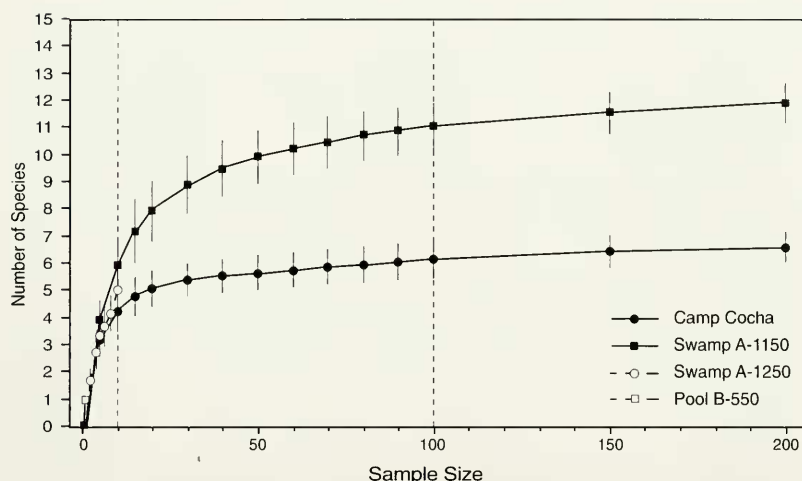
Fig. 13. Rarefaction curves for non-anuran species of the four study ponds. Error bars = ± 1 SD and vertical dashed lines indicate sample sizes of 10 (left) and 100 (right) individuals.

Table 6. Non-anuran species richness, abundance, evenness, and diversity in the four study ponds.

Pond	No. of species	No. of individuals	Rarefaction ($n = 10$)	Evenness (E)	Diversity (N1)	(N2)
Camp Cocha	7	845	4.27 ± 0.79	0.83	4.76	4.14
Swamp A-1150	13	547	5.91 ± 1.05	0.85	8.68	7.49
Swamp A-1250	5	11	5.00 ± 0.00	1.11	3.92	4.23
Pool B-550	1	10	1.00 ± 0.00	∞	1.00	1.00
Total	13	1413				

of species in common, followed by Swamp A-1250 and Camp Cocha, and Swamp A-1250 and Swamp A-1150, both with five. Pool B-550 had only one non-anuran species, the crab, but this species occurred in all the ponds.

In summary of biotic characteristics, Camp Cocha and Pool B-550 are similar in tadpole diversity, with both ponds being dominated by one common species (interestingly, a *Phyllomedusa* in both cases); however, these two ponds have no species of tadpoles in common. In addition, Camp Cocha had a much more diverse non-anuran fauna than Pool B-550; the two share only the single species of crab. Swamps A-1250 and A-1150 had a much higher tadpole diversity than the other two ponds—Swamp A-1250 because it had the greatest number of species, and Swamp A-1150 because

it had few tadpoles for the number of species. These two ponds, which were the most proximate pair, also had the greatest number of tadpoles in common. In terms of their non-anuran faunas, Swamp A-1150 is the most diverse, whereas Swamp A-1250 is the second lowest. These two ponds have a moderate number of non-anuran species in common.

Overall, the four study ponds display a range of abiotic and biotic characteristics. The following are the perfect rank correlations among the four study ponds for any of the biotic and abiotic characteristics. (1) The number of species of non-anurans, number of abundant species of non-anurans, size of pond, and depth of pond are correlated, and have a negative correlation to percentage light penetration. (2) Permanency and alkalinity/hardness are negatively correlated among ponds. (3) The number of species of adult frogs is correlated with the number of individual predators, and both are negatively correlated with evenness of predators. (4) The number of abundant species, number of very abundant species, and evenness of tadpoles are correlated. Clearly, many of the variables of these correlations are not independent, and the small sample size (four ponds) severely limits their interpretation. Furthermore, the absence of any correlation of tadpole richness, evenness, or diversity with any of the other aforementioned characteristics precludes any effort to explain the distribution of tadpole species among ponds in terms of these abiotic and biotic characteristics.

RESOURCE UTILIZATION

Macrohabitat

Twenty-nine of the 54 species (54%) at Cuzco Amazónico with life cycles that include an aquatic larval stage were observed at the study ponds as adults or tadpoles (Table 4). Thus, at least 25 species (46%) known in the local community were not present as adults or tadpoles, and thus presumably utilize either other macrohabitats or use the study ponds during other years or seasonal times. The latter possibility seems unlikely, however, because only Swamp A-1150 contained standing water beyond the study period.

Tadpoles of 10 of the 23 species of adults present were not found in the study ponds: These are *Bufo marinus*, *Ceratophrys cornuta*, *Hyla allenorum*, *H. schubarti*, *Leptodactylus leptodactyloides*, *L. petersii*, *Osteocephalus taurinus*, *Scarthyla ostinodactyla*, *Sciuax garbei*, and *Sphaenorhynchus lacteus*. Some of the latter occur at more than one of the study ponds. Adult *Leptodactylus petersii* were found at Camp Cocha and Swamp A-1150; likewise, adult *Osteocephalus taurinus* were found at Swamp A-1150 and Pool B-550. Adult *Scarthyla ostinodactyla* occurred at all study ponds except Pool B-550. There are several possible reasons for the absence of larvae of these taxa. The species may not have been breed-

ing. They might have bred, but their tadpoles might have been unsuccessful, or their tadpoles occurred in microhabitats other than those sampled. I know of only one case in which a species of tadpole occurred in a microhabitat not included in the transects, despite repeated sampling. *Scarthyla ostinodactyla* larvae were encountered in net sweeps away from the sampling transects amidst duckweed at the surface of Swamp A-1150.

Because some species occurred both as adults and tadpoles, but only as tadpoles in some ponds suggests differential success at macrohabitat utilization. Adult *Hyla parviceps* were found at Swamps A-1150 and A-1250, and Pool B-550, but no tadpoles were found at Swamp A-1150. Adult *Hyla fasciata* were found at Camp Cocha and Swamps A-1150 and A-1250, but tadpoles occurred only at Camp Cocha. Adult *Hyla koechlini* were seen at Camp Cocha and Swamps A-1150 and A-1250, but no tadpoles were found at Camp Cocha. Overall, Camp Cocha had the greatest number (8) of adults present for which tadpoles were not also found, followed by Swamps A-1150 and A-1250 with four each, and Pool B-550 with one.

Of the species of tadpoles collected, none occurred in all four study ponds, and only *Hamptophryne boliviana, Hyla brevifrons,* and *H.* cf. *leali,* occurred in three. Seven species occurred in two ponds, and nine in only one study pond. There seemed to be no consistent pattern in these occurrences among the ponds, except for the presence of four of those species that occur in a single pond (three of which were microhylids) in Swamp A-1250.

In summary, at Cuzco Amazónico nearly half of the anuran species with tadpoles did not utilize the study ponds during the study period. Species represented only by adults probably indicates the taxa were unsuccessful in recruitment or that they used other macrohabitats for breeding. The two largest ponds had the greatest number of adults present without tadpoles. These also had the greatest number of non-anuran individuals suggesting predation to be an important factor. None of the tadpoles is ubiquitous. In fact, only three species occur in three different ponds. Of the nine species that occur in only one pond, four occur in Swamp A-1250. There is differential utilization of study ponds, with adults, tadpoles, or both of different species at different ponds with no apparent pattern; this suggests differential use of the macrohabitats. The determinant factor of this differential use of macrohabitat from year to year by adults is beyond the scope of this study. It is possible that adult pond use varies from year to year and may contain a large stochastic component.

PHENOLOGY

Tadpoles of 35 of the 54 species of anurans at Cuzco Amazónico that have aquatic tadpoles were not encountered. Possibly some of these species breed at other times during the year (or at other sites as previously dis-

cussed). The timing restrictions of this study precluded determination of which species were not encountered because they breed during other time periods (i.e., beyond the rainy season), but they are probably few because of lack of aquatic macrohabitats beyond the rainy season at this relatively seasonal site.

Some species temporally partition the study ponds during the rainy season. At Camp Cocha, *Hamptophryne boliviana* and *Phyllomedusa vaillanti* were the only larvae present from mid-December until February (Fig. 8). *Phyllomedusa vaillanti* occurs through the entire study period, whereas *H. boliviana* was not found after January. The remaining species occurred sporadically during February (*Hyla leucophyllata, Altigius alios*) or March after the heaviest rains (*Hyla brevifrons, H. fasciata,* and Species A). A similar pattern was evident in Swamp A-1150 (Fig. 9). *Hamptophryne boliviana* and *Phyllomedusa vaillanti* were the first species to appear in mid-January. *Phyllomedusa vaillanti* occurred from mid-February to mid-March, whereas *H. boliviana* was not found after early February. Only one other species, *H. brevifrons,* occurred in January at Swamp A-1150, and did not occur again until mid-March, unlike at Camp Cocha where this species only occurred early in March. The remaining species at Swamp A-1150 occurred sporadically in February (*Hyla koechlini, H.* cf. *leali, Scinax icterica*) or February and March (*Hyla leucophyllata, Hyla* sp.) at times of the heaviest rains. Camp Cocha and Swamp A-1150 have some remarkable similarities. For example, *Hamptophryne boliviana* and *Phyllomedusa vaillanti* occurred before any other species in both ponds. Whereas *P. vaillanti* remained until the end of the study period, *Hamptophryne boliviana* disappeared midway through the study season, just prior to the heaviest rainfall, after which most of the other species appeared.

In Swamp A-1250, *Leptodactylus mystaceus* was the only species present in January, immediately after the swamp appeared (Fig. 10). Although the site nearly dried, these tadpoles were found in the remaining small puddles. At the beginning of February, after rains filled the swamp again, *L. mystaceus* was absent and, within 1 wk, seven other species appeared; four additional species appeared by the end of February. Most of these species were present well into March when the pond disappeared for the season, with the exception of the microhylids *Elachistocleis ovalis, Ctenophryne geayi,* and *Chiasmocleis ventrimaculata,* which were present for just a short period during the peak of the rainy season in the first half of February. The greatest number of larval species in Swamp A-1250 occurred in February when as many as seven species were collected on the same day. This may be characteristic of ephemeral swamps such as Swamp A-1250, where time is constrained and cannot be differentially utilized by species of tadpoles. Only *L. mystaceus* is absent during this time period, but faces the risk of premature drying of the pond earlier in the rainy season.

In Pool B-550, *Phyllomedusa tomopterna* and Species D were the first species to appear in late December (Fig. 11), and were the only species present until mid-January when *Colostethus marchesianus* appeared. The other two species, *Hyla parviceps* and *H.* cf. *leali,* first appeared in late January and early March, respectively. All species were present at the end of the study, when the pond was thoroughly netted in an attempt to remove all tadpoles. Like Camp Cocha, Pool B-550 had two species present early. Both of these species remained with additional rain that brought the three remaining species. The first occurrences of these additional species were staggered. All five species, once present, were continually encountered until the end of sampling.

At least some temporal partitioning of the aquatic habitats occurs during the rainy season at Cuzco Amazónico. Some species are probably opportunistic, breeding early, at first rains, and only once. Other species are present at the first accumulation of water, including *Hamptophryne boliviana* and *Phyllomedusa vaillanti* (Camp Cocha and Swamp A-1150), *Leptodactylus mystaceus* (Swamp A-1250), and *Phyllomedusa tomopterna* and Species D (Pool B-550). Of these, some (e.g., *Phyllomedusa tomopterna, P. vaillanti,* and Species D) persist, whereas others (e.g., *Hamptophryne boliviana* and *Leptodactylus mystaceus*) have transformed and left the ponds (and no further breeding) before additional heavy rains bring other species. Some species tend to have staggered arrival times (e.g., many species in Swamp A-1150 and Pool B-550), whereas others (e.g., *Ctenophryne geayi, Chiasmocleis ventrimaculata,* and *Elachistocleis ovalis* in Swamp A-1250) are present for limited periods of time at the peak of the rainy season. The ephemeral nature of some ponds seems to limit the degree to which temporal partitioning can take place and, thus, causes an increase in the number of temporally co-occurring species; this can be seen in Swamp A-1150 and Pool B-550. The length of time that ponds where available for tadpoles at Cuzco Amazónico may have been further constrained because of a shorter than average rainy season during the year of the study.

Microhabitat, diel activity, and development

Microhabitat.—Tadpoles were sampled from three levels in the water column representing three general microhabitats—surface, midwater, and bottom. These levels are a subset of the available microhabitats, and it should be noted that areas such as the littoral zone and areas of dense vegetation were not included and may be important components. Deviation from an even distribution among the levels was tested for nine species (those with $n \geq 15$), including two species (*Phyllomedusa vaillanti, Hamptophryne boliviana*) that occurred in two study ponds each (Table 7); these nine species accounted for 97% of all tadpoles sampled. All species

Table 7. Distribution of tadpoles among microhabitats. Dagger (†) indicates adjustment for schooling tadpoles. (See discussion in text.)

Species	n	Surface	Mid-level	Bottom	G	P
Camp Cocha						
Hamptophryne boliviana	39	13	15	11	0.618	0.7342
Phyllomedusa vaillanti	2318	365	1332	621	631.924	< 0.0001
Phyllomedusa vaillanti†	23	4	13	6	6.319	0.0424
Swamp A-1150						
Phyllomedusa vaillanti	55	4	7	44	51.382	< 0.0001
Swamp A-1250						
Chiasmocleis ventrimaculata	109	30	51	28	8.505	0.0142
Elachistocleis ovalis	38	13	12	13	0.053	0.9738
Hamptophryne boliviana	76	40	27	9	21.353	< 0.0001
Hyla koechlini	52	3	28	21	24.391	< 0.0001
Scinax icterica	299	48	108	143	50.454	< 0.0001
Pool B-550						
Hyla parviceps	38	9	10	19	4.528	0.1039
Phyllomedusa tomopterna	627	54	271	302	216.969	< 0.0001
Species D	61	4	16	41	36.830	< 0.0001

tested had tadpoles occurring at each level. Of the 11 tests, three species had distributions among the microhabitats that are not significantly differ-ent ($P \leq 0.05$) from an even distribution. These are *Hamptophryne boliviana* from Camp Cocha, *Elachistocleis ovalis* from Swamp A-1250, and *Hyla parviceps* from Pool B-550. The remaining eight tests showed significant deviations from an even distribution among levels.

In Camp Cocha the distribution of *Phyllomedusa vaillanti* among the levels was uneven ($P < 0.0001$), with 16% of the tadpoles occurring at the surface, 57% in the midlevel, and 27% at the bottom. This differs from the distribution of this species among levels in Swamp A-1150 with 7% at the surface, 13% in the midlevel, and 80% at the bottom, which was also significant ($P < 0.0001$). The larvae of *Phyllomedusa vaillanti* are unique among the species of tadpoles of this study because they are the only ones that school (Branch, 1983) and were observed doing this in both the Camp Cocha and Swamp A-1150. The G-test statistic used herein assumes inde-pendent observations, an assumption which is violated by schooling behav-ior; one should count individual schools and not individual tadpoles. As a conservative adjustment of the data, the tests were repeated with the counts adjusted by dividing by the school size, which was estimated in the field to

be approximately 100 individuals. With this adjustment, the distribution among levels in the Camp Cocha still remains significantly different from an even distribution ($P = 0.0424$). Too few tadpoles of *P. vaillanti* were sampled from Swamp A-1150 to adjust the test in this manner.

In Swamp A-1250, several larval species were unevenly distributed in the water column. In *Scinax icterica* ($P < 0.0001$), 16% of the tadpoles occurred at the surface, 36% in the midlevel, and 48% at the bottom. In *Hamptophryne boliviana* ($P < 0.0001$), 53% of the larvae were at the surface, 36% in the midlevel, and 12% at the bottom. This differs from the distribution of *H. boliviana* in Camp Cocha, where the larvae were evenly distributed through the water column. In *Hyla koechlini* ($P < 0.0001$), 6% of the tadpoles were at the surface, 54% in the midlevel, and 40% at the bottom, and in *Chiasmocleis ventrimaculata* ($P = 0.0142$), 28% were at the surface, 47% at midlevel, and 26% at the bottom. In Pool B-550, the larvae of *Phyllomedusa tomopterna* were distributed unevenly among the levels ($P < 0.0001$) with 9% at the surface, 43% in the midlevel, and 48% at the bottom. Similarly, the distribution of the unknown Species D was uneven ($P < 0.0001$) with 7% at the surface, 26% in midlevel, and 67% at the bottom of Pool B-550.

Of the eight tests with significantly uneven distributions through the water column, only *Hamptophryne boliviana* in Swamp A-1250 had the greatest frequency at the surface. All others (except *Chiasmocleis ventrimaculata*, which was close with the bottom having just two fewer individuals than the surface) frequented the surface microhabitat least. Only *Phyllomedusa vaillanti* in Camp Cocha and *Chiasmocleis ventrimaculata* and *Hyla koechlini* in Swamp A-1250 occurred most frequently in the midlevel. *Phyllomedusa vaillanti* in the Camp Cocha is particularly interesting because in Swamp A-1150 this species frequented the bottom most, although this observation might have been affected by schooling behavior. The remaining four tests with significantly uneven distributions had the greatest frequency of occurrence at the bottom, followed by midlevel and then surface, the most common distribution pattern.

Diel activity.—Tadpoles were sampled by day and night to determine if there was a preference of diel activity. Deviation from an even distribution of occurrence between day and night was tested in 12 species (those with *n* ≥ 10), including three species (*Phyllomedusa vaillanti, Hamptophryne boliviana, Hyla parviceps*) that occurred in two different study ponds each (Table 8); these 12 species accounted for 98% of all tadpoles sampled. Of the 15 tests, the diel distributions of six were the same by day and by night (*Elachistocleis ovalis* and *Hyla koechlini* in Swamp A-1250; *Colostethus marchesianus, Hyla parviceps, Phyllomedusa tomopterna,* and Species D in Pool B-550). The remaining nine tests showed significant ($P \leq 0.05$) deviations from an even diel distribution. *Hamptophryne boliviana* and

Table 8.   Distribution of tadpoles between day and night. Dagger (†) indicates adjustment for schooling tadpoles. (See discussion in text.)

Species	n	Day	Night	G	P
Camp Cocha					
Hamptophryne boliviana	39	6	33	20.578	< 0.0001
Phyllomedusa vaillanti	2318	1388	930	91.092	< 0.0001
Phyllomedusa vaillanti†	23	14	9	0.911	0.3398
Swamp A-1150					
Phyllomedusa vaillanti	55	1	54	66.250	< 0.0001
Hyla leucophyllata	12	0	12	16.636	< 0.0001
Swamp A-1250					
Chiasmocleis ventrimaculata	109	25	84	33.713	< 0.0001
Elachistocleis ovalis	38	19	19	0	1.0000
Hamptophryne boliviana	76	12	64	39.062	< 0.0001
Hyla koechlini	52	20	32	2.794	0.0946
Hyla parviceps	10	1	9	7.361	0.0067
Leptodactylus mystaceus	14	2	12	7.925	0.0049
Scinax icterica	299	23	276	252.331	< 0.0001
Pool B-550					
Colostethus marchesianus	11	8	3	2.358	0.1246
Hyla parviceps	38	14	24	2.663	0.1027
Phyllomedusa tomopterna	627	330	297	1.738	0.1874
Species D	61	27	34	0.805	0.3696

Phyllomedusa vaillanti from Camp Cocha, *Hyla leucophyllata* and *Phyllomedusa vaillanti* from Swamp A-1150, and five species from Swamp A-1250 (*Chiasmocleis ventrimaculata, Hamptophryne boliviana, Hyla parviceps, Leptodactylus mystaceus,* and *Scinax icterica*) were captured more commonly at night. Only *Hyla leucophyllata* occurred exclusively during one time period (night). *Phyllomedusa vaillanti* in Camp Cocha was the only species that was more frequent (60%) by day.

Schooling behavior in tadpoles such as *Phyllomedusa vaillanti* often is explained as a predator avoidance mechanism (studies cited in Branch, 1983). This could explain the ability of *Phyllomedusa vaillanti* to exploit the resources during the day because of its lowered risk to visually oriented predators such as fish. However, when the data are adjusted for schooling (as for the test of distribution among microhabitats), the test fails to find significant differences ($P = 0.3398$) between diurnal and nocturnal larval distributions in Camp Cocha.

Of the other species that occur in two ponds, nearly the same proportion occurred at night and day for *Hamptophryne boliviana* in both Camp

Cocha and Swamp A-1250. *Hyla parviceps* was more frequent at night in both Swamp A-1250 and Pool B-550, although the difference was not significant ($P = 0.1027$) in the latter. *Phyllomedusa vaillanti* occurred more frequently by day in the Camp Cocha, but by night in Swamp A-1150.

Interrelationship of microhabitat, diel activity, and development.— In order to determine the presence, and nature, of interaction among level occupied by the larvae in the water column, diel activity, and development, a Log-Linear Model Analysis was performed on data for those individual species from individual ponds with sufficient sample size. Log-Linear Model Analysis tests for interactions among attributes (= nominal variables) of a contingency table by measuring the relative ability of various models, each sequentially including fewer combinations of variables, to fit expected values to those observed. This analysis requires that all cells in the observed data matrix have non-zero frequencies, that the expected cell frequencies of the model with the best fit are no less than one, and that no more than 20% of the cells have frequencies of less than five. Most species had inadequate sample sizes, but others were rendered usable by combining categories of developmental stages or day and night.

There are sufficient data for five species from three ponds to examine using Log-Linear Model Analysis—*Phyllomedusa vaillanti* from Camp Cocha; *Chiasmocleis ventrimaculata, Hamptophryne boliviana,* and *Scinax icterica* from Swamp A-1250; and *Phyllomedusa tomopterna* from Pool B-550 (Tables 9–13). It should be noted that Log-Linear Model Analysis assumes independent observations which may not be true for *P. vaillanti,*

Table 9. Data table used for 3-way Log-Linear Model Analysis of *Phyllomedusa vaillanti* from Camp Cocha.

Stage	Diel period	Level Surface	Level Midlevel	Bottom	Total
≤ 28	Day	213	807	194	1214
	Night	108	365	285	758
	Total	321	1172	479	1972
29–34	Day	25	84	43	152
	Night	16	56	66	138
	Total	41	140	109	290
35–40	Day	0	9	12	21
	Night	3	10	20	33
	Total	3	19	32	54
Total		365	1331	620	2316

Table 10.	Data table used for 3-way Log-Linear Model Analysis of *Chiasmocleis ventrimaculata* from Swamp A-1250.

Stage	Diel period	Level Surface	Midlevel	Bottom	Total
≤ 28	Day	2	0	1	3
	Night	11	16	8	35
	Total	13	16	9	38
29–40	Day	4	11	7	22
	Night	13	24	12	49
	Total	17	35	19	71
Total	Total	30	51	28	109

so this analysis should be interpreted with the knowledge that schooling behavior may have confounded the results.

Camp Cocha Phyllomedusa vaillanti: Analysis of 2316 individuals of *Phyllomedusa vaillanti* from Camp Cocha (Table 9; note one cell with a frequency of 0) reveals a non-significant 3-way interaction ($P = 0.1112$; Table 14), but significant associations between each pair of variables. This indicates that the degree of association between any pair of variables is the same over (unaffected by) the level of the third, but the third variable is conditionally dependent on each of the other two variables. The associations between each pair of variables are discussed separately.

Stage and level association (Fig. 14A): There is a significant association between larval stage and level in the water column ($P < 0.0001$; Table 14). As previously demonstrated in the microhabitat section, most tadpoles of *Phyllomedusa vaillanti* in Camp Cocha occurred at midlevel, then bottom, and the fewest at the surface. This was the case for the earliest stage (≤ 28) with 59% at midlevel, 24% at the bottom, and 16% at the surface. However,

Table 11.	Data table used for 2-way Log-Linear Model Analysis of *Hamptophryne boliviana* from Swamp A-1250.

Stage	Surface	Midlevel	Level Bottom	Total
≤ 28	23	17	3	43
29–34	9	7	4	20
35–40	8	3	2	13
Total	40	27	9	76

Table 12. Data table used for 2-way Log-Linear Model Analysis of *Scinax icterica* from Swamp A-1250.

Stage	Surface	Midlevel	Level Bottom	Total
≤ 25	13	36	47	96
26–28	28	49	62	139
29–31	1	14	21	36
32–34	5	5	12	22
35–37	1	4	1	6
Total	48	108	143	299

at later stages, the proportion of tadpoles occurring at the bottom level increases, whereas the proportion at midlevel and surface decreases. At the most advanced developmental stages (35–40), most tadpoles occurred at the bottom (59%), then midlevel (35%), and the least at the surface (6%).

Diel and level association (Fig. 14B, C): There is a significant association between diel activity and level in the water column ($P < 0.0001$; Table 14). At surface and midwater, more tadpoles occurred by day than at night (65 and 68% respectively), whereas at the bottom more occurred at night (60%). Among levels, the greatest number of tadpoles occurred at midlevel, then bottom, and least at the surface for both day and night, although the relative proportions differ, with a lower proportion at the surface and midlevel and a greater proportion at the bottom at night versus day.

Table 13. Data table used for 3-way Log-Linear Model Analysis of *Phyllomedusa tomopterna* from Pool B-550.

Stage	Diel period	Surface	Level Midlevel	Bottom	Total
≤ 28	Day	15	117	107	239
	Night	29	96	155	280
	Total	44	213	262	519
29–40	Day	2	9	9	20
	Night	3	7	7	17
	Total	5	16	16	37
Total		49	229	278	556

Table 14.   Results of 3-way Log-Linear Model Analyses. The variables of the models are: D = diel, L = level, S = stage.

Model	df	*Phyllomedusa vaillanti* Camp Cocha			df	*Chiasmocleis ventrimaculata* Swamp A-1250			df	*Phyllomedusa tomopterna* Pool B-550		
		G	P			G	P			G	P	
L	15	3134.15	0.0000		9	57.97	0.0000		9	516.20	0.0000	
D	16	3674.25	0.0000		10	32.76	0.0003		10	705.57	0.0000	
S	15	921.82	0.0000		10	56.33	0.0000		10	209.40	0.0000	
L,D	14	3042.97	0.0000		8	24.26	0.0021		8	513.60	0.0000	
D,S	14	830.65	0.0000		9	22.61	0.0071		9	206.80	0.0000	
S,L	13	290.55	0.0000		8	47.82	0.0000		8	17.43	0.0259	
L,D,S	12	199.38	0.0000		7	14.11	0.0493		7	14.83	0.0382	
LD	12	2906.82	0.0000		6	23.57	0.0006		6	501.58	0.0000	
LS	9	242.02	0.0000		6	46.53	0.0000		6	16.15	0.0130	
DS	12	812.05	0.0000		8	14.11	0.0790		8	205.91	0.0000	
L,DS	10	180.78	0.0000		6	5.60	0.4692		6	13.95	0.0302	
D,LS	8	150.85	0.0000		5	12.82	0.0251		5	13.55	0.0187	
S,LD	10	63.23	0.0000		5	13.42	0.0197		5	2.81	0.7297	
LD,LS	6	14.70	0.0228		3	12.14	0.0069		3	1.53	0.6763	
LS,DS	6	132.25	0.0000		4	4.31	0.3653		4	12.67	0.0130	
DS,LD	8	44.63	0.0000		4	4.92	0.2958		4	1.92	0.7503	
LD,LS,DS	4	7.51	0.1112		2	3.75	0.1535		2	0.60	0.7404	

Stage and diel association (Fig. 14D): There is a significant association between larval stage and diel activity (*P* = 0.0228; Table 14). As previously demonstrated more *P. vaillanti* tadpoles occur by day than at night in Camp Cocha. This is true for the earliest stage (≤ 28), with 62% occurring during the day. However, at later stages, the proportion of tadpoles found at night increases, such that at the highest stage (35–40), most (61%) occur at night.

As noted above, this analysis must be interpreted with caution because the assumption of independent observations required by Log-Linear Model Analysis is suspect because of the schooling behavior of *Phyllomedusa vaillanti* tadpoles. In spite of this restriction, the associations between variables seem to be explained by this schooling behavior. The size-class schools would be expected to become smaller as they age owing to anticipated mortality of tadpoles. It seems logical that as schools diminish in size, they would perform less effectively as anti-predator mechanisms. Therefore, one might anticipate that older tadpoles not protected by schooling would be less active by day, and might occur more frequently at the bottom, thereby remaining inconspicuous to visually oriented predators such as fish. Both of these patterns were illustrated by the associations among stage and level, and stage and diel demonstrated by the Log-Linear
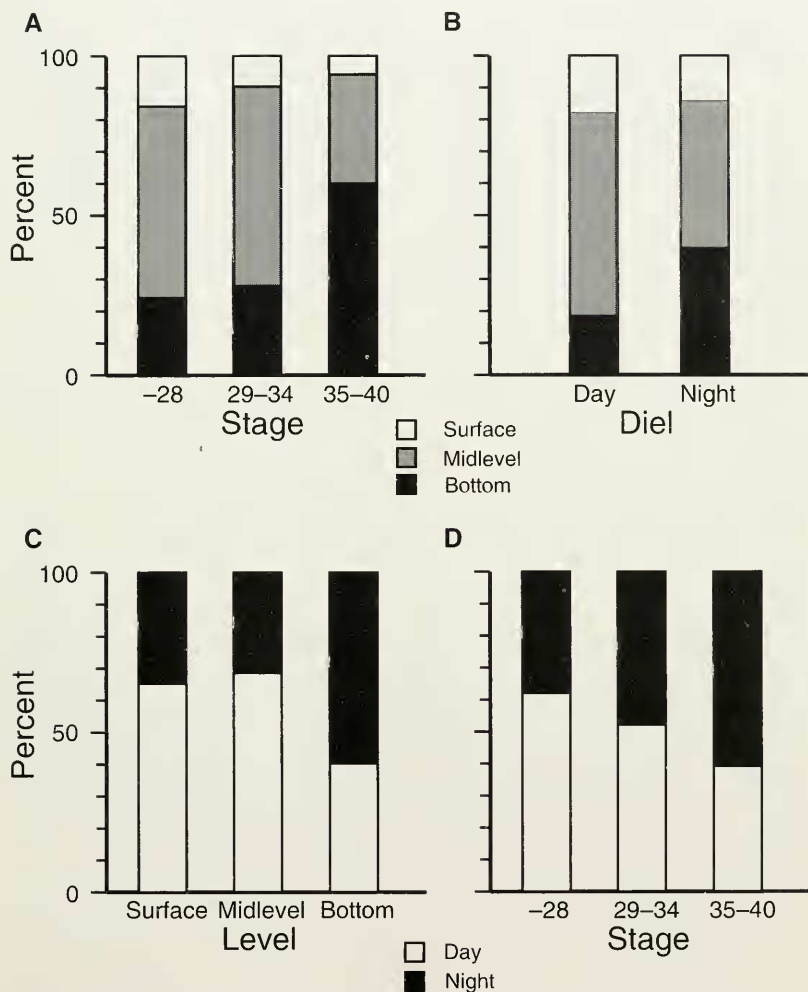
Fig. 14.   Associations between the variables larval stage and level in water column (A), diel time period and level in water column (B-C), and larval stage and diel time period (D) for *Phyllomedusa vaillanti* from Camp Cocha.

Model Analysis. Another possibility is that because the *P. vaillanti* tadpole schools apparently disassociate at night (Branch, 1983; although I have seen some schools at night), one might expect proportionately fewer in the midlevel, where schools are active, and more at the bottom. This association between diel and level also was revealed by the analysis. Again, owing to analytical restrictions, further study that specifically focuses on *P. vaillanti* schooling at Cuzco Amazónico is necessary before we clearly understand the dynamics of this schooling behavior.
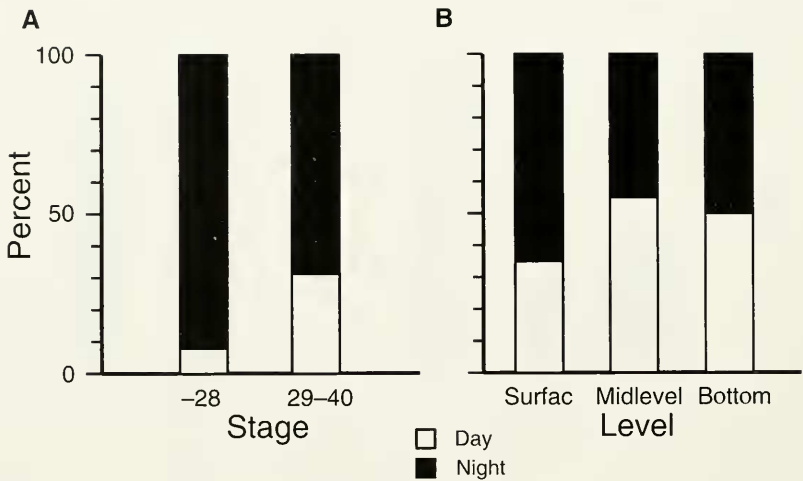
Fig. 15.   Association between the variables stage and diel for *Chiasmocleis ventrimaculata* of Swamp A-1250 (A), and between the variables level and diel for *Phyllomedusa tomopterna* from Pool B-550 (B).

Swamp A-1250 Chiasmocleis ventrimaculata: Analysis of the data for *Chiasmocleis ventrimaculata* from Swamp A-1250 (Table 10) revealed that level in the water column is completely independent of diel activity and larval stage ($P = 0.4692$; Table 14), and that the latter are dependent ($P = 0.0069$), regardless of level. Overall (summed over all stages and diel), more tadpoles occurred at midlevel (47%), then surface (28%), and fewest at the bottom (26%). More tadpoles occurred at night regardless of stage (77%), but the proportion decreased with increasing stage (Fig. 15A).

Swamp A-1250 Hamptophryne boliviana: Only 16% of *Hamptophryne boliviana* tadpoles occurred during the day; therefore, day and night were combined for 2-way Log-Linear Model Analysis (Table 11), which revealed that larval stage and level in the water column are independent ($P = 0.5047$; Table 15). As described above, significantly more tadpoles occurred by night than by day, but because day and night were combined for this analysis, the relationship of diel activity with larval stage or level in the water column cannot be addressed. As previously shown, the most tadpoles occurred at the surface, then midlevel, and the fewest at the bottom, with the proportions varying with little pattern among stages.

Swamp A-1250 Scinax icterica: Only 8% of the *Scinax icterica* tadpoles were collected during the day; therefore, day and night were combined for a 2-way Log-Linear Model Analysis (Table 12). Analysis revealed that larval stage and level in the water column might be independent ($P = 0.0839$; Table 15). As described above, significantly more tadpoles occurred by night than by day, but because day and night were combined for

Table 15. Results of 2-way Log-Linear Model Analyses. The variables of the models are: L = level, S = stage.

Model	*Hamptophryne boliviana* Swamp A-1250			*Scinax icterica* Swamp A-1250		
	df	G	P	df	G	P
L	6	22.03	0.0012	12	231.16	0.0000
S	6	24.68	0.0004	10	64.37	0.0000
L,S	4	3.33	0.5047	8	13.92	0.0839

analysis, the relationship of diel activity with larval stage or level in the water column cannot be addressed. Also previously shown, *S. icterica* tadpoles were encountered most frequently on the bottom, then the midlevel, and the fewest at the surface, with the proportions varying just slightly among stages.

Pool B-550 Phyllomedusa tomopterna: Analysis of the data for *Phyllomedusa tomopterna* from Pool B-550 (Table 13) revealed that larval stage is completely independent of diel activity and level in the water column ($P = 0.7297$; Table 14), and that level and diel activity are conditionally dependent given stage ($P = 0.0130$). Surface (65%) and bottom (58%) levels have more tadpoles by night, whereas at midlevel, more tadpoles occurred by day (55%), (Fig. 15B). As described above, overall, the greatest proportion of tadpoles occurred at the bottom, then midlevel, and the fewest at the surface. These proportions varied just slightly between day and night; by day, slightly more occurred at midlevel.

In summary, many species of tadpoles have level and diel biases. Tadpoles of almost all species occurred most frequently at the bottom or middle of the water column. Only one species (*Phyllomedusa vaillanti*) occurred most frequently by day, and this may be explained by unique schooling behavior. In some species, these level and diel biases are associated with each other and/or developmental stage. In other species, these variables seem unrelated. These associations can differ for a species among ponds.

FEEDING MORPHOLOGY

Types and sizes of food particles were not examined in this study. To address differences in feeding preferences among species, I categorized tadpoles into ecomorphological guilds of exotrophic tadpoles that inhabit nonflowing aquatic systems, as described by Altig and Johnston (1989).

These categories are based on morphological differences (particularly of the oral apparatus), microhabitat position, and sometimes behavior. It should be emphasized that this is a coarse-grained examination of feeding, based on the assumption that different guilds eat different food types and/ or sizes. It should be recognized that these guilds are defined partly by microhabitat position and, therefore, are not completely independent of other resource dimensions.

The tadpoles from the four study ponds represent five ecomorphological guilds—viz., Suspension Feeder Type 2; Macrophagous Type 2—Nektonic; Nektonic Type 1; Suspension-Rasper; and Benthic (Table 16). Only one species, Species A, could not be placed in a guild. The two guilds with the greatest number of species were Suspension Feeder Type 2 (Microhylidae) and Macrophagous Type 2—Nektonic (*Hyla leucophyllata* and *H. parviceps* groups), followed by Nektonic Type 1 and Benthic, both with three species, and Suspension-Raspers (*Phyllomedusa*) with two.

The most frequent guild was Macrophagus Type 2—Nektonic, which was the only guild represented in each pond (Table 17). Both Suspension

Table 16.   Ecomorphological guilds of tadpoles from the study ponds at Cuzco Amazónico.

Guild	Species
Suspension Feeder Type 2	*Chiasmocleis ventrimaculata*
	Ctenophryne geayi
	Elachistocleis ovalis
	Hamptophryne boliviana
	Altigius alios
Macrophagous Type 2—Nektonic	*Hyla brevifrons*
	Hyla koechlini
	Hyla cf. *leali*
	Hyla leucophyllata
	Hyla parviceps
Nektonic Type 1	*Hyla fasciata*
	Scinax icterica
	Hyla sp.
Suspension-Rasper	*Phyllomedusa tomopterna*
	Phyllomedusa vaillanti
Benthic	*Colostethus marchesianus*
	Leptodactylus mystaceus
	Species D

Table 17.   Distribution of ecomorphological guilds among the study ponds.

Guild	Camp Cocha	Swamp A-1150	Swamp A-1250	Pool B-550	Total
Suspension Feeder Type 2	2	1	4	0	7
Macrophagous Type 2—Nektonic	2	4	4	2	12
Nektonic Type 1	1	2	2	0	5
Suspension Rasper	1	1	0	1	3
Benthic	0	0	2	2	4

Feeder Type 2 and Nektonic Type 1 were absent from Pool B-550, whereas Suspension-Raspers were absent from Swamp A-1250, and Benthic was absent from the two largest ponds—Camp Cocha and Swamp A-1150. Overall, the guilds seem to be distributed fairly evenly among ponds in which they occur, with the only exception being the abundance of Suspension Feeder Type 2 in Swamp A-1250. Suspension-Raspers (*Phyllomedusa tomopterna* and *P. vaillanti*) never occurred together in a pond.

None of the ponds had tadpoles from all five guilds. The same four guilds were represented in the two largest swamps, Camp Cocha and Swamp A-1150, although the number of species in each guild differed between the two ponds (Table 17). Also, neither of these two ponds had any benthic tadpole species. Swamp A-1250 was unique in that four Suspension Feeder Type 2 tadpole species occurred there; all were microhylids, three of which were not found in any other pond. In addition, Swamp A-1250 is the only pond that lacked any Suspension-Raspers (*Phyllomedusa*), whereas Pool B-550 lacked any members of the Suspension Feeder Type 2 and Nektonic Type 1 guilds, both of which were well represented in other ponds.

In summary, it seems that guilds are fairly evenly distributed among ponds. This is consistent with differential utilization of food resources by feeding morphology. Some guilds occur primarily in certain types of ponds, such as Suspension Feeders Type 2 (microhylids) in the ephemeral Swamp A-1250. Others are not found in particular types of ponds, such as the absence of Benthic tadpoles from the larger swamps (Camp Cocha, Swamp A-1150), and Suspension Feeder Type 2 and Nektonic Type 1 from the small Pool B-550.

Niche Breadths

Niche breadths were calculated as a general measure of each species' utilization of all resource states. Levins' (1968) measure was chosen because it estimates the uniformity of distribution of individuals among resource states and it is one of the more commonly used niche breadth measures. The resource states included in the analysis were all possible combinations of ponds, levels in the water column, diel time period, and months—a total of 96 resource states, 23 of which had no occurrences, leaving a total of 73 for analysis. Thus, the resource states incorporate macrohabitat, microhabitat, diel time period, and temporal dimensions. Niche breadths were calculated for both tadpoles and non-anuran species (Tables 18, 19).

No species was ubiquitous across niche space, and most species had narrow breadths, representing usage of a restricted number of resource states. In general, tadpoles had narrower breadths ($\bar{x} = 0.059 \pm 0.055$) than did the non-anuran species ($\bar{x} = 0.137 \pm 0.107$). The greatest breadths were for the two species of insects, Nepidae sp. and *Belostoma* sp. with 0.331 and 0.292, respectively, and the one species of trichodactylid crab with 0.239. The niche breadths of the fish were much closer to those of the tadpoles. *Pterolebias* sp. had the greatest niche breadth for fish with 0.142. Among the tadpoles, *Phyllomedusa vaillanti, Hyla parviceps,* and *Phyllomedusa tomopterna* had the greatest breadths with 0.188, 0.155, and 0.130, respectively. Niche breadth is not consistently correlated with sample size, and species from the temporary ponds do not necessarily have greater niche breadths.

Niche Overlaps

To compare species utilization of all resource dimensions, I calculated niche overlaps (Morista, 1959) for anuran and non-anuran species using the same resource states employed for calculating niche breadths. Two hundred and thirty-nine of 496 comparisons had non-zero overlaps. The overlaps were examined in three different categories: anurans with anurans, anurans with non-anurans, and non-anurans with non-anurans. In spite of having lower niche breadths, anurans with anurans had the highest mean overlap ($\bar{x} = 0.464 \pm 0.382$), whereas the anurans with non-anurans had the lowest ($\bar{x} = 0.100 \pm 0.137$); non-anurans with non anurans were intermediate ($\bar{x} = 0.400 \pm 0.333$). This is not surprising because widely different types of organisms (tadpoles vs. fish and insects) would be expected to utilize resources quite differently.

Seventeen tadpole overlaps were greater than one standard deviation from the mean (Table 20). Among these, the *Hyla brevifrons* × *Hyla* sp. overlap was by far the highest (greater than two standard deviations from the mean); however, these species represent different ecomorphological

Table 18. Levins' measure of niche breadth for tadpoles.

Species	Niche breadth
Phyllomedusa vaillanti	0.188
Hyla parviceps	0.155
Phyllomedusa tomopterna	0.130
Species D	0.094
Hamptophryne boliviana	0.080
Colostethus marchesianus	0.063
Hyla brevifrons	0.062
Elachistocleis ovalis	0.060
Hyla leucophyllata	0.053
Chiasmocleis ventrimaculata	0.045
Hyla koechlini	0.045
Hyla cf. *leali*	0.045
Hyla sp.	0.036
Scinax icterica	0.028
Leptodactylus mystaceus	0.025
Ctenophryne geayi	0.011
Hyla fasciata	0.000
Altigius alios	0.000
Species A	0.000

Table 19. Levins' measure of niche breadth for non-anuran species.

Species	Niche breadth
Nepidae sp.	0.331
Belostoma sp.	0.292
Trichodactylidae sp.	0.239
Pterolebias sp.	0.142
Pyrhulina sp.	0.139
Cynolebias sp.	0.110
Characidae Species A	0.084
Carnegiella sp.	0.082
Characidae Species C	0.056
Characidae Species B	0.031
Species A	0.000

guilds. Only four of the 17 high overlaps are between species of the same ecomorphological guild: *Colostethus marchesianus* × Species D, *Hyla brevifrons* × *H. koechlini*, *Elachistocleis ovalis* × *Chiasmocleis ventrimaculata*, and *Scinax icterica* × *Hyla* sp. Thus, these are identified as potentially competitive associations. Most overlaps among anuran with

Table 20.   Moristas' measurement of niche overlap for anuran species pairs with overlaps greater than one standard deviation from the mean. Dagger (†) indicates species pairs from the same ecomorphological guild.

Overlap	Species
1.943	*Hyla brevifrons* × *Hyla* sp.
1.141	*Scinax icterica* × *Hyla* sp.†
1.060	*Hyla koechlini* × *Hyla* sp.
0.965	*Hyla brevifrons* × *Hyla koechlini*†
0.950	*Chiasmocleis ventrimaculata* × *Hyla brevifrons*
0.936	*Hyla* cf. *leali* × Species D
0.910	*Hyla parviceps* × Species D
0.908	*Hyla* cf. *leali* × *Colostethus marchesianus*
0.905	*Chiasmocleis ventrimaculata* × *Hyla koechlini*
0.895	*Chiasmocleis ventrimaculata* × *Hyla* sp.
0.893	*Colostethus marchesianus* × Species D†
0.879	*Elachistocleis ovalis* × *Chiasmocleis ventrimaculata*†
0.877	*Phyllomedusa tomopterna* × *Hyla parviceps*
0.875	*Elachistocleis ovalis* × *Hyla koechlini*
0.858	*Hyla koechlini* × *Scinax icterica*
0.855	*Phyllomedusa tomopterna* × Species D
0.851	*Chiasmocleis ventrimaculata* × *Scinax icterica*

Table 21.   Morista's measurement of niche overlap for anuran and non-anuran species pairs with overlaps greater than one standard deviation from the mean.

Overlap	Species
0.496	*Hyla leucophyllata* × *Pyrhulina* sp.
0.492	*Hyla leucophyllata* × *Carnegiella* sp.
0.469	*Hyla brevifrons* × Characidae Species C
0.458	*Hyla brevifrons* × *Callichthys callichthys*
0.425	*Hyla brevifrons* × Characidae Species A
0.401	*Phyllomedusa vaillanti* × Trichodactylidae sp.
0.388	*Hyla brevifrons* × Nepidae
0.382	*Hamptophryne boliviana* × *Pyrhulina* sp.
0.368	*Phyllomedusa vaillanti* × *Pyrhulina* sp.
0.352	*Hyla brevifrons* × Characidae Species B
0.322	*Hyla leucophyllata* × *Belostoma* sp.
0.313	*Hyla leucophyllata* × Nepidae sp.
0.293	*Hamptophryne boliviana* × *Cynolebias* sp.
0.269	*Phyllomedusa vaillanti* × Nepidae sp.
0.269	*Phyllomedusa vaillanti* × *Pterolebias* sp.
0.255	*Phyllomedusa vaillanti* × *Cynolebias* sp.
0.252	*Hyla leucophyllata* × Characidae Species A
0.239	*Phyllomedusa vaillanti* × *Callichthyes callichthyes*

non-anuran species were much lower than those for anurans with anurans (Table 21). Likewise, the greatest of these represent candidates for predatory or competitive interactions.

DISCUSSION

Resource Utilization

Patterns of differential resource utilization among species of tadpoles at Cuzco Amazónico are evident for most of the resource dimensions studied. Macrohabitat and seasonal time seem to be the most important dimensions, followed by food, microhabitat, and diel time period.

The occurrence of tadpoles in a particular pond (macrohabitat) depends on adults successfully breeding and depositing eggs, and survival of at least some of the tadpoles. Those species present only as adults were not breeding (e.g., *Bufo marinus*, *Ceratophrys cornuta*, and *Osteocephalus taurinus*), had eggs or tadpoles that were not successful, or had tadpoles that used microhabitats not sampled (e.g., *Scarthyla ostinodactyla* at the surface in duckweed of heavily vegetated areas). It is unlikely that many species were not sampled, because many areas of all the study ponds were netted, and this sampling effort produced species other than those encountered in the sampling transects only once (*Scarthyla ostinodactyla* as mentioned above). It is possible that the study ponds did not possess the major characteristics associated with the primary adaptive pond type of each of the species present only as adults (Heyer, 1976). That is, these "missing" species use other types of macrohabitats successfully, and the characteristics of the study ponds precluded these species from successful breeding or recruitment by these species. This also might explain why some species with adults present in several ponds had tadpoles in only some of the ponds.

An affinity for a particular pond type was observed in *Scarthyla ostinodactyla*. Adults of this species were present at three of the study ponds, but tadpoles were found only among duckweed at the surface of Swamp A-1150; there was less extensive duckweed in the other ponds. It seems that this component of aquatic vegetation is an important characteristic of breeding ponds for *S. ostinodactyla*. Likewise, four species of microhylids occurred in the most temporary swamp, Swamp A-1250. Heyer (1973) proposed that selection for reduction of time of larval life is correlated with uncertain aquatic habitats because of sporadic rainfall. He suggested that the predominance of microhylids in the frog fauna at Sakaerat Thailand, where there are primarily temporary pools, was because the larval periods of microhylids are shorter relative to those of most other frogs (see also Gascon, 1991.) Gascon (1991) reported that among the many aquatic habitats at his site in Amazonian Brazil, individual species responded to habitat characteristics and bred at sites with specific at-

tributes, and that there were no large-scale species assemblages that covaried in habitat use. This finding also seems to characterize Cuzco Amazónico, where few species are widespread among the study ponds, many species are found only in a single pond, and there seems to be no species assemblages that covary in occurrence among ponds. Thus, the presence of adults at a macrohabitat does not necessarily indicate that tadpoles will be present, because species differ in their requirements and ability to breed and successfully recruit in various types of ponds. These observations suggest that the anuran species at Cuzco Amazónico indeed do utilize macrohabitats differentially; however, the limited number of macrohabitats investigated here precludes identification of the specific biotic and abiotic characteristics that are influential. It is possible that there is a large stochastic element determining what adults breed at each of the ponds, and that this could be expected to vary from year to year. A clearer understanding will come from studies that include adult breeding and measure many aspects of many ponds (e.g., Gascon, 1991), ideally for multiple years.

Differential temporal utilization of the study ponds in the current study was limited to within the rainy season. Some species, such as the two species of *Phyllomedusa*, occur throughout the rainy season. Other species are more limited temporally; examples are *Osteocephalus taurinus*, which breeds only at the very first heavy rains (W. E. Duellman pers. comm.), or most of the microhylids in Swamp A-1250, which breed only at the peak of the rainy season. Various annual breeding patterns of anurans have been documented at other Amazonian sites (Crump, 1971; Duellman, 1978; Toft and Duellman, 1979; Aichinger, 1987); these include continuous, opportunistic, and sporadic breeders (Crump, 1974). In addition, as suggested by Gascon (1991), different cues are used by different species for the onset of reproduction. He found that some species cue by time, rather than rainfall. The temporal restrictions of this study precluded the recognition of any species that breed outside the rainy season. However, these species probably are rare because Cuzco Amazónico is relatively seasonal and few aquatic macrohabitats are present during the dry season. A similar situation was reported by Aichinger (1987) at Panguana, where the availability of aquatic breeding sites restricted the reproductive activities of anurans to the rainy season. This, however, differs from other tropical localities (Hero, 1990; Gascon, 1991) where some of the same species that breed only during the rainy season at Cuzco Amazónico are known to breed continuously (e.g., *Colostethus marchesianus*, *Phyllomedusa tomopterna*, and *P. vaillanti*).

Which resource dimension—macrohabitat or time—is most important at Cuzco Amazónico? The most important dimension is the one which is

utilized differentially by the greatest number of species. Perhaps the dimension that can explain the absence of the 25 species from the study ponds should be considered particularly important. These missing species must either use other ponds (macrohabitats) or occur at other times (seasons). The data from this study indicate that macrohabitat is potentially more important than time. Seasonal partitioning does not seem to be possible at Cuzco Amazónico because of the absence of aquatic habitats outside of the rainy season. Temporal partitioning is limited to within the rainy season. On the other hand, a number of species are known to use macrohabitats other than the study ponds (e.g., *Bufo typhonius* and *Hyla calcarata,* which breed at the slow-moving stream). Toft (1985) pointed out a widely observed phenomenon in resource-partitioning studies—namely, that organisms that can use a wider range of a resource also may partition it to a greater degree. The opposite seemed to be the case with temporal utilization at Cuzco Amazónico during the study period; given that only a narrow range of a resource (time) was available, it could not be partitioned to a great degree. This is clearly illustrated in the most temporary pond, Swamp A-1250, in which there were more temporally co-occurring species than in the more permanent Camp Cocha and Swamp A-1150.

The conclusion that macrohabitat is more important than seasonal time at Cuzco Amazónico conflicts with the many studies included in Toft's review, for which seasonal time was considered the most important dimension in aquatic larval assemblages. Seasonal time is certainly important at Cuzco Amazónico, but because of unavailability of aquatic habitats outside the rainy season, the degree to which this resource can be partitioned is limited. This is generally true at temperate or dry tropical localities. Because the rainy season was much drier than average and was essentially abbreviated by 2 mo, it is not surprising that the degree to which time was differentially utilized by species in the current study was limited. During a year when rainfall is closer to average, temporal partitioning may be more important than found in this study. It is possible that during the study period, many of the "missing" species never bred because they did not receive the cues that would occur with more rain and a longer rainy season. In addition, more rain might permit some aquatic habitats such as Camp Cocha to maintain water into the dry season. On the other hand, a more typical rainy season might result in more macrohabitats, thereby allowing species to partition this resource dimension to a greater degree. Furthermore, depending on the conditions, species may not breed every year. It is difficult to determine which dimension is most important, projecting beyond the data for this single study period. As suggested by Heyer (1976), studies spanning several years are required to determine the relationship between climate and breeding phenology. It is clear that rainfall can influ-

ence the degree to which resource dimensions, particularly time, can be utilized differentially, and it seems probable that the most important resource dimension varies with climatic fluctuations from year to year. This may be quite important at Cuzco Amazónico, which is situated near the transition from humid to dry tropical forest and experiences significant annual variation in rainfall in addition to seasonality. Thus, Cuzco Amazónico has less predictable aquatic habitats (annually as well as seasonally) than many other tropical rainforest localities, and in its seasonality resembles situations found in more temperate climates.

If oral morphology (ecomorphological guild) reflects differences in feeding, food appears to be an important resource dimension at Cuzco Amazónico, principally because the greatest overlaps (similar temporal and spatial occurrences) tend to be between species that differ in ecomorphological guild. In addition, because each pond contains a variety of ecomorphological guilds, it seems that food is utilized differentially within each pond. This analysis of utilization of food resources is based on the assumption that morphology reflects differences in ingestion of food-particle type and/or size. Further studies on the relationship between oral morphology of tadpoles and food particle type and size ingested are needed. Heyer (1973) found that scraping feeders ingest smaller particles than the beakless feeders, but this may be the result of food processing prior to ingestion, rather than selecting different-sized particles. Altig and Johnston (1989) cautioned that the relationship of tadpole oral morphology to feeding methodology is not clear, and that there is danger with predicting function and ecological latitude solely from morphology. They also pointed out that stringent partitioning of food resources among tadpoles has not been demonstrated, and proposed that the non-reproductive, temporary inhabitants that feed low on the food chain with abundant types and amounts of food indeed do not demand stringent or continuous partitioning. Food-resource partitioning may occur only in rare, extremely harsh situations, but it then could be influential. Thus, interpretation of the variety of oral morphologies among the larvae in the study ponds, as reflecting differential use of food resources must be done with caution.

Microhabitat and diel time period are not used very differently by the various species of tadpoles, with almost all species occurring most frequently at the bottom or midlevel and at night. The single species that occurs by day (*Phyllomedusa vaillanti*) possesses a unique schooling behavioral that may permit exploitation of the pond by day without danger of predation. In addition, some species showed associations among diel period of activity, level, and developmental stage, suggesting the possibility that there is ontogenetic changes in species utilization of microhabitats and diel time periods.

In summary, macrohabitat and time are the two most important resource dimensions. During the study period, macrohabitat appeared to be more

important than time because temporal partitioning was limited to the rainy season. However, this may differ year to year in response to climatic variation, specifically rainfall. Food seems important, given the assumption that species with different oral morphologies consume different food particle types or sizes. Microhabitat and diel time period are the resource dimensions used least differently, although they may be associated with one another and, moreover, change with development for a particular species.

CAUSAL FACTORS

The data of this study are inadequate to determine with confidence which, and to what extent, the various causal factors are responsible for the observed patterns of resource utilization. However, it seems likely that predation is more influential than competition. Rainfall seems to be the most influential factor in determining the patterns of resource utilization.

Interpreting the role of competition in these tadpole assemblages from the data reported herein requires that we assume that (1) differences in feeding morphology reflect differences in food ingestion, and (2) greater overlaps indicate greater potential for present competition than lower overlaps. Given these assumptions, it would seem logical to conclude that the absence of many high overlaps between species of similar morphology indicates that competition, or at least the potential for it, is rare. On the other hand, low overlaps may be the result of competition. The data reported herein are inadequate to differentiate the two possibilities and to confidently justify the assumptions and interpret the niche overlap values in terms of competition. Predation, on the other hand, seems likely to influence the tadpole assemblage, simply because many of the fish and aquatic insect species present are known predators and likely feed on tadpoles. The factor most influential in determining patterns of resource utilization at Cuzco Amazónico seems to be rainfall, primarily because it determines the degree to which the macrohabitats can be utilized temporally. Similarly, the single physical factor of rainfall distribution regulates anuran reproductive patterns at other worldwide tropical localities with a pronounced dry season (e.g., Dixon and Heyer, 1968; Heyer, 1973; Wiest, 1982; Aichinger, 1987; Hero, 1990).

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